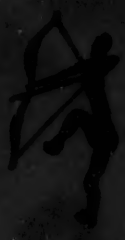
HUMAN BIOLOGY

a record of research

SEPTEMBER, 1954

UNIVERSITY OF MICHIGAN
JAN 3 1955
MEDICAL

Vol. 26 No. 3



PUBLISHED QUARTERLY BY
WAYNE UNIVERSITY PRESS, DETROIT 1, MICHIGAN, U.S.A.

HUMAN BIOLOGY

a record of research

FOUNDED BY RAYMOND PEARL

Editor

GABRIEL W. LASKER

in association with

BENTLEY GLASS — DONALD MAINLAND

JAMES N. SPUHLER — WILLIAM L. STRAUS, JR.

Review Editor

JOSEF BROŽEK

HUMAN BIOLOGY is published quarterly by Wayne University Press, Detroit 1, Michigan, U. S. A. The advance subscription price is $5.00 a year (foreign postage 35 cents; Canadian 15 cents). Single current issues are $2.00, plus postage.

Subscribers should notify the publishers of change in address at least two weeks before publication of the issue with which the change is to take effect. No claim for non-receipt of an issue will be entertained unless made immediately upon receipt of the next succeeding issue.

Manuscripts and communications regarding editorial matters should be addressed to Editor, Human Biology, Department of Anatomy, Wayne University College of Medicine, 1401 Rivard St., Detroit 7, Michigan.

WAYNE UNIVERSITY PRESS, *Publishers*

4841 Cass Avenue

DETROIT 1, MICHIGAN, U. S. A.

Entered as second class matter at the post office at Detroit, Michigan. Accepted at the special rate of postage under section 34.40(e) P. L. & R. authorized.

Copyright 1954 by Wayne University Press

EARNEST ALBERT HOOTON

A DEDICATION

On May 1st, 1954, physical anthropology lost one of its most versatile and renowned leaders, Earnest Albert Hooton, Professor of Anthropology, Harvard University. It is with a deep feeling of appreciation that we who participated in this symposium join in dedicating the published version to his memory.

Dr. Hooton's position in the world of primatology was indeed a unique one for although his scientific writings cover a wide scale, he never contributed an original research paper dealing with a non-human primate. Yet his position was secure for he had with considerable success brought together and published in a popular, scientific manner much of the available information on "Man's Poor Relations." The publication of this book and the interest which he engendered in his students for non-human relatives have done much to establish primatology as a means of gaining perspective of the general problems of psychology, anthropology, and related sciences.

It was for these reasons that Dr. Hooton was requested to prepare the opening paper of this symposium. The other contributors were asked because of their special qualifications on some specific facet of the general topic. But the aim of the symposium was not only to bring together the palaeontology, comparative anatomy, anthropology, and psychology of the non-human primates but also to indicate how such knowledge can contribute to our understanding of the problems of human evolution. Such wide and, in a sense, nebulous aims would be foredoomed to utter failure unless the deeper and unifying aspects of the studies could be clearly and precisely stated. This was one of the final tasks which Dr. Hooton performed with his usual thoroughness: a thoroughness which gave the necessary coherence and meaning to the symposium as a whole.

Having witnessed the success with which Dr. Hooton handled his difficult role, the contributors dedicate this symposium to his honor. We hope that interest shown by the listening audience is indicative of a wider, growing interest in primatology which will remain as a lasting tribute to Dr. Hooton's efforts.

James A. Gavan
Medical College of South Carolina
Charleston, S. C.

UNIVERSITY OF MICHIGAN LIBRARIES

HUMAN BIOLOGY
a record of research

SEPTEMBER, 1954

VOL. 26 No. 3

THE IMPORTANCE OF PRIMATE STUDIES IN ANTHROPOLOGY

BY EARNEST HOOTON
Harvard University

ANTHROPOLOGY is the study of man, but difficulties have been encountered in formulating a satisfactory scientific definition of man. Huxley's "erect and featherless biped" apparently harks back to Plato, for Diogenes Laertius (*circa* A. D. 200) says: "Plato having defined man to be a two-legged animal without feathers, Diogenes plucked a cock and brought it into the Academy, and said, 'This is Plato's man.' On which account this addition was made to the definition—'with broad flat nails.'" As emended, this might include also the anthropoid apes. The most liberal definition of man with which I am familiar is that of Shaw, propounded in his introduction to "Back to Methuselah." He characterizes man as "only an amoeba with acquirements." This seems to me to be going a bit too far down the animal line, in addition to smacking of Lamarckianism.

The contention that we must settle upon a definition of man before

we can delimit the scope of anthropology is, however, something more than a semantic quibble. Efforts to separate man from other primates, by adding to Plato's qualifications for humanity other requisites, such as articulate speech, the possession of a soul, the development of a culture (whatever that is), etc., are too vague for usefulness and merely lead to further definitions, dialectics, and hair-splittings. Even the famous dictum that man is "the only animal that drinks when he isn't thirsty and makes love all the year round" does not rid us of the company of the great apes, nor even of the less socially acceptable monkeys.

There is, in point of fact, a rather serious disagreement as to the human or infra-human status of the erect, presumably featherless, biped Australopithecinae of South Africa, who almost certainly had feet modified away from the prehensile type for support in two-legged locomotion, who probably used sticks and stones with their emancipated fore-limbs, who satisfied the minimal and some further dental requirements for human status and yet seem to have had such small brains that their hats would not have slipped down over the ears of a chimpanzee. If these Australopithecinae were men, we shall have to enlarge the zoological scope of anthropology.

However, I do not really worry about the Australopithecinae—whether they were ape men or merely man apes—nor about any of these other taxonomic questions, which I have raised principally as the exhibition of that interest in terminology necessary to qualify myself as a social scientist. While the invention of a new term to describe old things might enhance the valuation of this preamble to a couple of days of papers on apes, monkeys, and their ilk, I shall fall back upon the use of the word "primatology." This term, although repellant and linguistically a hybrid, is redeemed if not legitimated by a dual connotation: the study of the highest animal order and the study which of all the -ologies is, or ought to be, *primus*, prime, or first in importance.

For it is my contention that Departments of Primatology should be established, not only as separate sections of our great research institutions, but also as teaching divisions in our universities. I shall endeavor to support this proposal, however, solely by pointing out how basic to the understanding of anthropology, sociology, psychology, and all of the other disciplines that pertain to man, is the investigation with every possible scientific technique and method of the primate animals grouped by Linnaeus and his successors in the order that includes man.

THE IMPORTANCE OF PRIMATE STUDIES TO PHYSICAL ANTHROPOLOGY AND TO GENERAL BIOLOGY

Taxonomy

Taxonomy, which assigns man and all other animals to their proper pigeon-holes in the zoological filing cabinet, has become somewhat neglected in these days when anatomists prefer to be histologists and when zoologists are preoccupied with biochemistry, physiology, and endocrinology. Yet our weariness with the eternal wrangling over what constitutes a species, or a subspecies, must not blunt a keen realization of the continuing importance of researches in comparative anatomy and comparative physiology. The essay published by Edward Tyson in 1699, "Orang-Outang, sive Homo Sylvestris, or the Anatomy of a Pygmie compared with that of a Monkey, an Ape, and a Man," is one of the greatest achievements of science leading to an understanding of higher primate evolution. We cannot all be Tysons, but the rewarding task of comparing the apes and the more important monkeys with each other system by system is not merely incomplete; it has hardly been begun. In fact, there is not even one great anthropoid ape whose anatomy has been completely described, to say nothing of the intercomparisons with other genera.

Human Evolution

The foundations and the main structural features of the theory of human evolution are built up from the materials furnished by primatology. Apart from the general body of anatomical and physiological knowledge appertaining to all of *Homo sapiens* or modern man, which is utilizable as the human frame of reference in taxonomy and comparative anatomy, there is little, in fact almost nothing, in the anthropology of recent *Homo sapiens* that contributes substantially to the theory of man's evolution from other primate forms. There are no stages of human evolution discernible in the anatomy and physiology of recent man; only variations, mosaics of progressive and retrogressive characters, and a blurred picture of continuing differentiation, either without direction or possibly degenerative. We have to go back to the anatomically archaic forms of man, rather ponderously called palaeanthropic, before the accumulating evidence of an origin in apelike forms becomes plausible, and to the study of contemporary great apes and fossil apes before that evidence becomes impressive and conclusive.

The anatomist or anthropologist who attempts to reconstruct the skull

and the postcranial skeleton of a palaeanthropic type of man without a sound knowledge of the anatomy of the great apes and of at least the Old World monkeys is really only a sort of chiropractor operating in a situation where the patient cannot complain and the injury done to science, while not fatal, results in the mutilation of fact and the perversion of theory. Ignorance and naiveté do not excuse anyone for concocting hypothetical human ancestors from a few surviving bony fragments, with the help only of a couple of dissecting room skulls, a text-book of anatomy, and perhaps the cranium of one miserable chimpanzee. Piecing together the skeletal remains of *Homo sapiens* is not much more difficult than mending a pot, and missing parts may be restored with some confidence. But doing this job on, for example, the Australopithecinae requires a knowledge of infra-human primate anatomy possessed by few scientists in our time aside from Sir Arthur Keith and Adolph Schultz.

In figuring out the anatomical reconstruction and physiological interpretation of such post-cranial parts as the spine, the foot, and the pelvis, in forms so remote from modern man as are these South African ape men or man apes, a knowledge of human and anthropoid ape anatomy is insufficient. It has to be supplemented, as William Straus and other astute students know, by a thorough familiarity with the anatomy and the mechanics of posture and gait in terrestrial quadrapedal primates such as the baboon.

I need not labor this point further, but I cannot refrain from remarking that many persons who write eruditely and definitively upon the minutiae of dental morphology in ancient man and other animals, who do not hesitate to draw phylogenetic conclusions from a variation in form of the wrinkles separating molar cusps, and all that sort of stuff, overlook the fact that there does not exist as yet even an adequate, much less an exhaustive, description of the dentition of the common or garden chimpanzee, based upon any reasonably large series of specimens.

The range of variation of ape characters is extremely wide. In a Peabody Museum collection of some 300 chimpanzee crania from a restricted area in Liberia, this extensive variation manifests itself not only in dentition, but in cranial morphology and brain size. There are in this collection chimpanzees with sagittal crests, such as are supposed to occur only in male gorillas and male orang-utans. The cranial capacity varies so much that the uppermost limit overlaps the range of the gorilla. Ought we to build a towering structure of human phylogeny

upon the sands of ignorance of primate anatomy? We do not know enough about the anatomy and dentition of existing primates safely to interpret those of fossil primates, proto-human or infra-human. We sorely need dozens of trained investigators in the field so richly cultivated by Adoph Schultz; it is far too big and too important for even this great anthropologist to work alone.

Human Physiology and Pathology

The science of physiology progresses largely by the use of experimental animals. The results of experiments upon and observations of the physiological processes of lower animals are utilized in human contexts. It seems reasonable to suppose that the closer the experimental animal is to man, structurally and physiologically, the more accurately will the experimental findings apply to man, whether in physiology or pathology. Among the most important physiological discoveries of the century, as respects its anthropological significance, and in the field of immunology, must be reckoned the antigens or blood substances, including the standard ABO blood groups, the MN, the Rh system, and others that are now too numerous to mention. The finding of blood substances among the great apes identical with, or closely similar to, those in man, made necessary a radical revision of theories of the date of origin and the prehistoric processes of diffusion of the human ABO blood groups and their genes. For example, it rendered untenable the theory that the New World was peopled from Asia before the mutations that originated the A and B substances (the p and q genes) merely because it was thought that all American Indians of unmixed blood belonged to group O. The accidental discovery of the Rh factor, derived from serological abuse of the humble rhesus monkey, has ramified into a complex system, which has great promise of significance in the determination of racial differences. Perhaps even more important is the discovery that the Rh factors and, by inference, many other blood properties are not, as previously supposed, biologically neutral or indifferent, but that, on the contrary, they may be vital factors in the selection for survival or extinction of the animal that possesses them. It seems probable that a much more extensive use of primate material not only in serological studies, but in the whole area of human physiology and biochemistry, might throw a brighter and clearer light upon human problems than is shed by depending upon one-candle experimental lower animals. It is realized that anthropoid apes are expensive, slow-breeding, and, in some cases almost impossible to raise in capitivity, but these

and the postcranial skeleton of a palaeanthropic type of man without a sound knowledge of the anatomy of the great apes and of at least the Old World monkeys is really only a sort of chiropractor operating in a situation where the patient cannot complain and the injury done to science, while not fatal, results in the mutilation of fact and the perversion of theory. Ignorance and naiveté do not excuse anyone for concocting hypothetical human ancestors from a few surviving bony fragments, with the help only of a couple of dissecting room skulls, a text-book of anatomy, and perhaps the cranium of one miserable chimpanzee. Piecing together the skeletal remains of *Homo sapiens* is not much more difficult than mending a pot, and missing parts may be restored with some confidence. But doing this job on, for example, the Australopithecinae requires a knowledge of infra-human primate anatomy possessed by few scientists in our time aside from Sir Arthur Keith and Adolph Schultz.

In figuring out the anatomical reconstruction and physiological interpretation of such post-cranial parts as the spine, the foot, and the pelvis, in forms so remote from modern man as are these South African ape men or man apes, a knowledge of human and anthropoid ape anatomy is insufficient. It has to be supplemented, as William Straus and other astute students know, by a thorough familiarity with the anatomy and the mechanics of posture and gait in terrestrial quadrapedal primates such as the baboon.

I need not labor this point further, but I cannot refrain from remarking that many persons who write eruditely and definitively upon the minutiae of dental morphology in ancient man and other animals, who do not hesitate to draw phylogenetic conclusions from a variation in form of the wrinkles separating molar cusps, and all that sort of stuff, overlook the fact that there does not exist as yet even an adequate, much less an exhaustive, description of the dentition of the common or garden chimpanzee, based upon any reasonably large series of specimens.

The range of variation of ape characters is extremely wide. In a Peabody Museum collection of some 300 chimpanzee crania from a restricted area in Liberia, this extensive variation manifests itself not only in dentition, but in cranial morphology and brain size. There are in this collection chimpanzees with sagittal crests, such as are supposed to occur only in male gorillas and male orang-utans. The cranial capacity varies so much that the uppermost limit overlaps the range of the gorilla. Ought we to build a towering structure of human phylogeny

upon the sands of ignorance of primate anatomy? We do not know enough about the anatomy and dentition of existing primates safely to interpret those of fossil primates, proto-human or infra-human. We sorely need dozens of trained investigators in the field so richly cultivated by Adoph Schultz; it is far too big and too important for even this great anthropologist to work alone.

Human Physiology and Pathology

The science of physiology progresses largely by the use of experimental animals. The results of experiments upon and observations of the physiological processes of lower animals are utilized in human contexts. It seems reasonable to suppose that the closer the experimental animal is to man, structurally and physiologically, the more accurately will the experimental findings apply to man, whether in physiology or pathology. Among the most important physiological discoveries of the century, as respects its anthropological significance, and in the field of immunology, must be reckoned the antigens or blood substances, including the standard ABO blood groups, the MN, the Rh system, and others that are now too numerous to mention. The finding of blood substances among the great apes identical with, or closely similar to, those in man, made necessary a radical revision of theories of the date of origin and the prehistoric processes of diffusion of the human ABO blood groups and their genes. For example, it rendered untenable the theory that the New World was peopled from Asia before the mutations that originated the A and B substances (the p and q genes) merely because it was thought that all American Indians of unmixed blood belonged to group O. The accidental discovery of the Rh factor, derived from serological abuse of the humble rhesus monkey, has ramified into a complex system, which has great promise of significance in the determination of racial differences. Perhaps even more important is the discovery that the Rh factors and, by inference, many other blood properties are not, as previously supposed, biologically neutral or indifferent, but that, on the contrary, they may be vital factors in the selection for survival or extinction of the animal that possesses them. It seems probable that a much more extensive use of primate material not only in serological studies, but in the whole area of human physiology and biochemistry, might throw a brighter and clearer light upon human problems than is shed by depending upon one-candle experimental lower animals. It is realized that anthropoid apes are expensive, slow-breeding, and, in some cases almost impossible to raise in capitivity, but these

obstacles would be surmounted if there were enough interest in their use for these purposes. That interest can be aroused only if the special value of infra-human primate physiology is recognized as bearing upon similar processes in human beings. Of course, monkeys and lower primates still are much cheaper to keep and much more rapid to reproduce, but, as far as I am aware, only the rhesus monkey is commonly used as a laboratory animal.

Some years ago Dr. S. Zuckerman, having reported a number of inter-generic and inter-specific crosses in the primate order that were recorded in the London Zoological Gardens, informed me in conversation of his desire and intention to carry on breeding and race-crossing experiments with lower primates, especially lemurs. Apparently this project never came to fruition. But *why* cannot genetic studies be made upon the lower primates? Must we forever depend upon genetic inferences carried over the vast chasm that yawns between man and the drosophila? Of course, rats, rabbits, and guinea pigs are zoologically more relevant to man than fruit flies, but do we not perhaps omit something very important when we fail to act upon the reasonable supposition that the genetics of the order to which we belong, even of the more remote genera and species of that order, are probably more closely applicable to our species than the genetics of lower mammals or of insects?

The study of human growth changes has been vitalized in recent decades by the use of x-ray methods and by physiological interpretations made possible by advances in endocrinology. In early days, the comparatively sterile studies of growth yielded little more than annual increments of anthropometric measurements and smoothed curves. The study of age changes from maturity to senility urgently demands the attention of medical and anthropological investigators, and not much has been done about it in the way of organized research. Both types of investigation, involving the development and maturation of the human organism and its gradual deterioration and disintegration, could be helped and accelerated, in my opinion, by the use of parallel studies upon infra-human primates—apes and monkeys. The latter could be subjected to experimental procedures that we hardly venture to try upon our own children or those of any other human parent. Such growth studies of the chimpanzee as have been carried out by Nissen, Gavan, and others in the Yerkes Laboratory at Orange Park have been, it seems to me, of enormous interest and value.

THE IMPORTANCE OF PRIMATE STUDIES TO CULTURAL ANTHROPOLOGY AND, IN GENERAL, TO THE UNDERSTANDING OF HUMAN BEHAVIOR

Man's use of tools and weapons has usually been considered as one of his prime distinguishing characteristics, and so it is. However, the manual equipment of the infra-human primates is, in some genera and species, only a little inferior to that of man. All of you are familiar with the contributions of Koehler, Yerkes, and other students of primate psychology to the use of tools by chimpanzees and other infra-human primates. These studies have great significance with reference to the beginning of tool-using in our early human and proto-human ancestors. But more intensive investigations of tool- and weapon-using in apes and monkeys are needed and it would seem that the relationship of brain and general neurological development to the tool-using capacity might be studied with profit.

The ever-intriguing Australopithecinae had possibly arrived at an evolutionary status in which they were using tools of the ready-made kind and were perhaps even attempting to alter natural objects the better to serve such purposes. How large a brain, or how complicated a nervous organization, is required to effect the transition between using natural objects and fabricating or trying to make tools and weapons? We need the primatologist in trying to solve this problem.

Social anthropology and sociology have been so greatly enriched by studies of the family life and social habits of infra-human primates, notably those of Yerkes, C. R. Carpenter, S. Zuckerman, and Henry Nissen, that it seems superfluous to coment in any detail upon them. I shall no doubt evoke the indignant disagreement of social anthropologists when I suggest that more is to be learned about the genesis of the human family and the beginning of social organization and community life in early man by the study of contemporary infra-human primates living under natural conditions than by the studies of retarded human groups living today under conditions variously described as "primitive," "uncivilized" or "savage." In my time I have read a fair number of excellent anthropological monographs dealing with these modern "primitives" or "pre-literates"—all the way from the Negrito, the Bushman, and the Australian upward to higher levels of material culture and social organization (if one may be permitted to imply that there are different levels). Far be it from me to impugn the value of these studies, but these contemporary savages are not "primitive," not on the evolutionary

upgrade, not the stuff of which societal progress is made. Whether environmentally underprivileged or genetically underendowed, or both, they are cultural imbeciles or morons—at any rate if we believe our "civilizations" are superior to their rude ways of life. If they are too smart to "fall for" our higher cultures, they are that much further from our ancestral prototypes.

To me, what Carpenter tells us about the family life of the gibbon, and the contrasts between the group and individual life of, first, the Hamadryas baboon, then the macaque, and then the howling monkey, are far more instructive for the history of the prehuman, proto-human and early human social groupings than any of the stuff on present-day savages written by anthropologists.

Of course these splendid pioneer studies of the behavior of infra-human primates in the wild have already been incorporated into the basic literature of anthropology. But I view with utmost dismay the lack of sustained interest in such studies, the present reluctance of institutions to promote them, and the difficulty of financing them, which I assume to be the reason for their discontinuance by Carpenter and for the failure of other younger men to take them up where he has left off. I know of no studies bearing upon man's cultural and social origins that have been begun so brilliantly, that have progressed so magnificently, and that have been abandoned so miserably and ignominiously. It is as if one were to dig for oil, strike a gusher, and then immediately cap it up and go away and forget about it. Anthropology needs more studies of primate sociology.

Personality, Temperament, and Intelligence

The studies of primate intelligence, personality, and temperament so painstakingly and successfully conducted by experimental animal psychologists in the past 30 years and more are just as interesting and important to the anthropologists as to any psychologist. It will be a serious detriment to the development of anthropology if the interests of psychologists in this field of investigation flag or lapse, as I sometimes fear to be the case. It may be pointed out that of the anthropoid apes, only the chimpanzee has received any considerable amount of attention in this respect. I do not, of course, forget the splendid studies of Yerkes on Julius the Orang and on the young female gorilla, Congo. Other isolated studies might be mentioned, all invaluable to the student who feels that a knowledge of the psychology of the primates is necessary

for the interpretation of human mental development. It should be clear that everything known to us about individual morphological variation in the higher primates, especially the great apes, leads to the surmise that they must differ individually so widely in temperament, in intelligence, and in personality that many studies of single subject apes will be required to establish the ranges and the norms. Probably newer and better techniques of studying the individuality of apes and monkeys will bring us even more valuable insights into the interrelationship of body and mind within the same species.

I presume that the specialties of linguistics, phonetics, neurology and neuro-anatomy have developed a long way since primate investigators first tackled the problem of the capacities of the great apes for articulate speech. The subject urgently requires further study and experimentation.

Conclusion

Recent man and his fossil precursors may be taken to represent the apex and the uppermost courses of a primate pyramid, the bottom of which was laid down in the Eocene, a matter of 60 millions of years ago. Some existing forms represent survivors from all or nearly all of the successive courses topped by man. There are many fragmentary blocks in each of these courses and some are missing entirely. These are the extinct primate forms, a few preserved in part as fossils. Every system of the human organism—skeletal, muscular, circulatory, digestive, nervous or what not—is built upon its precursors in the underlying layers. Every detail of each system and every variation has originated in one or other of the lower courses. If we are to understand man, if we are to be anthropologists in a real sense of the term, our knowledge of every aspect of the human organism and its functioning should extend downward to its lower primate origin. We can leave the earlier precursors of our order to the general zoologists and to the palaeontologists.

If anthropology is going to amount to anything as a complete science of man, it will have to avoid splitting itself up into specialties that tend to secede and join up with other disciplines—such as social anthropology going over to sociology and social psychology, physical anthropology to human anatomy and general biology, archaeology to fine arts and history. These fissions and new agglutinations result principally in dismembering man and his behavior, pushing Humpty Dumpty off the wall, so that nowhere is there to be found a comprehensive treatment of the total human animal. The way of salvation for anthropology lies in main-

taining its unity, even though the title is pretentious and overambitious for the present coverage by a few practitioners. But under this all-inclusive name anthropologists can welcome to their hospitable board all sorts of other scientists, who may not only sit with them and put their feet under the anthropological table, but are also privileged to bring with them their own provender, of which the sponsoring anthropologists gladly and greedily partake. So in this symposium on primate studies, sponsored by anthropology, the contributors are psychologists, palaeontologists, geologists, dental specialists, human anatomists, comparative anatomists, serologists, and one or two anthropologists. We appreciate what our colleagues bring to us and they can find perhaps a warmer reception here for their primate studies than in their own specialties. We do not proselytize; we do not want to seduce them away from their own disciplines, but we insist upon regarding them as true, full-fledged anthropologists. Paraphrasing some Roman or other we anthropologists say: *Primatus sum, nihil primatum mihi alienum puto,* which, being translated, is "I am a primate; nothing about primates is outside of my bailiwick."

FOSSIL PRIMATES IN THE NEW WORLD
(ABSTRACT)

BY G. L. JEPSEN

Department of Geology, Princeton University, Princeton, N. J.

ONLY three orders of living mammals, the marsupials, insectivores, and carnivores, have longer geological histories than the primates whose oldest known members occur in North America in sediments of mid Paleocene age,—about 65 million years ago. These earliest prosimians, mostly tree-living fruit-eaters, are distributed among five families and present many intricate problems of origin and distribution. Their relationships among themselves and to the living prosimians of the Old World and to the anthropoids of both hemispheres are obscure.

Two of these early families, the Carpolestidae and the Phenacolemuridae were exclusively North American in distribution and became extinct in the early Eocene. A third family, the Plesiadapidae, has a similar range in North America but it survived a little longer in Europe, after appearing there in the late Paleocene. Members of the other two families, the highly specialized Apatemyidae and the tarsiiform Anaptomorphidae lived continuously in North America, for a period of about 30 million years, until early Oligocene time. They also inhabited Europe during the Eocene, and, in this epoch a sixth prosimian family, the Adapidae, appeared in both North America and Europe.

There is no record of primates in North America from the early Oligocene to the time of human occupation, a gap of approximately 35 million years. However, in South America a few fossil platyrrhine monkeys of Miocene age have been found in Patagonia and Colombia, and an extinct genus, Pleistocene or recent in age, from Jamaica brings a record of fossil anthropoids closer to North America. All these forms (the total is only a few fragments representing three or four genera)

were apparently closely related to the living ceboids and marmosets, and do not indicate their relationships to the earlier North American groups or to Old World primates. The platyrrhines were probably derived, however, from some part of the North American early Tertiary prosimian stock that reached South America by land in the Paleocene or by raft somewhat later.

A few more than 100 genera of extinct primates are now known. Most of these, about 70, are prosimians (tupaioids, lemuroids, and tarsioids) which are represented by a few more genera in the New World than in the Eastern Hemisphere. Only one genus, an early Tertiary form, occurred on both sides of the Atlantic.

The distribution pattern of the genera of prosimians in North America and Europe suggests some interesting speculations. In North America the number of genera of primates increased rapidly from the earliest appearance in the mid Paleocene to the greatest figure, 13, in the early Eocene, and then declined. In Europe the rise to the same maximum number of genera was a little later and the disappearance occurred even faster.

Evidence from fossil plants of a temperature increase in North America between early Paleocene and late Eocene time might be correlated with the increase of the prosimians, and their decline may have been the result of selective competition in the great evolutionary surge of the rodents, which had earlier overcome the multituberculates, in mid and late Eocene time.

THE GEOLOGIC HISTORY OF NON-HOMINID PRIMATES IN THE OLD WORLD

BY BRYAN PATTERSON

Chicago Natural History Museum

DISAGREEMENTS among students of the primates are many and profound—a statement that hardly possesses the charm of novelty. Since these disagreements extend to what should and what should not be included in the order both at the bottom and, in the family Hominidae, at the top, it becomes necessary at the outset to define the term "non-hominid primate." In this discussion, it will include the tupaioids and exclude the *Australopithecus* group. As thus limited, the topic is a very large one, requiring for thorough treatment far more space than can be allotted here. In an attempt to cover as much ground as possible, the setting in which Old World primate history unfolded will be touched upon, the nature of the fossil record reviewed, some points in it singled out for mention, and, in conclusion, a brief discussion given of certain theoretical interpretations that seem reasonable in the light of the knowledge now available.

THE SETTING

The evolution of the primates in the Old World took place over the greater part of Eurasia and Africa. We may confidently infer that this immense area has always been diverse climatically and topographically, although not as much so, as regards climate at least, in the earlier Tertiary as during the latest Tertiary, Pleistocene, and Recent periods. It was, however, much more cut up at various times in the past than it is now. A great negative belt in the earth's crust extended across it from the Atlantic to the Pacific. This was the site of the Tethys Sea, of which the Mediterranean is a remnant, a major barrier during much

of the Tertiary to free faunal interchange between Europe and Northern Asia, on the one side, and Africa and Southern Asia, on the other. This barrier, of course, was neither complete nor continuous; the constant inflow of sediment combined with temporary cessation or slowing of subsidence here and there would have resulted in temporary land connections or insular stepping stones at various places along its enormous length. There were other negative belts, small only in comparison with the Tethys, that played their parts in the fragmentation process; to name only one, I may mention the Uralian trough, which occupied roughly the present site of the Ural mountains and served for some time as a partial barrier to east-west faunal movements in the northern mass. In addition to the long continuing, although not continuous, barriers presented by the negative belts, parts of the land areas were at times flooded by shallow epicontinental seas that must effectively have isolated areas of higher ground. Western Europe, for example, must have been an archipelago several times in its history. Concurrently with these ever-changing relations between land and sea, climatic fluctuations certainly took place, together with concomitant changes in the distribution of forest and savannah, steppe and arid region. Under such conditions, ranges would be shifted, contracted, or expanded; contiguous regions would be sundered, perhaps fragmented, to remain separated for longer or shorter periods of time and then to be reunited. This would seem to be true especially for the earlier part of the Tertiary. As time went on, the area became progressively more unified. Conditions, in short, were excellent for evolutionary diversification. With Old World primate evolution occurring in a setting such as this, it is difficult to take seriously the pronouncements so frequent in the literature that this or that group of primates arose in this or that region—certainly not in the present very sketchy state of our knowledge.

THE NATURE OF THE RECORD

Just how sketchy this knowledge is, a glance at the map (fig. 1) reveals. The various symbols show, very roughly, the distribution of fossil primate finds in space and time. They designate regions rather than specific localities and it was unfortunately not possible on this scale to indicate what part of an epoch the symbols represent. A jibe frequently leveled at distribution maps is that what they really show is the distribution of collectors, not that of organisms. The charge must be fully admitted in this instance. Only in Western Europe, the region

FIG. 1. OCCURRENCES OF NON-HOMINID FOSSIL PRIMATES IN THE OLD WORLD.

longest and most intensively worked, do we have anything that even remotely approaches a continuous record. The scarcity of records from the other, much larger, regions stands out in striking contrast. Europe contains the only Paleocene locality that has yielded primates, and there also is found the only Eocene sequence. Extra-European Eocene localities number but two, both Late: one in northern China and one in Burma. All we know about primate life in the Oligocene is derived from a few finds in Egypt and Central Asia. Were it not for the East African Miocene, our records for this epoch would be meager indeed. The Pliocene is represented by relatively abundant although fragmentary material from India; elsewhere chiefly by various finds in Europe, including one new one of outstanding importance—the new material of *Pliopithecus*. Pleistocene symbols are more numerous than any others on the map, but this is unfortunately no indication that our knowledge of the primates of this epoch is adequate. The fact is that nearly everywhere, Western Europe excepted, the surface has barely been scratched.

Going on a consideration of the number of genera known (table 1), the deficiencies of our knowledge become even more apparent. There are 43 genera of living Old World non-hominid primates, give or take a few in either direction, according to taste in lumping or splitting. About 60 extinct genera are known, approximately half again as many as the living. This small total becomes even less impressive when we reflect that the vast majority are known only from fragments of mandibles and maxillaries. The number of forms of which we have a fair knowledge of skull structure and/or some acquaintance with the postcranial skeleton is far fewer. The roll of these is soon called. Paleocene: *Plesiadapis* (from North American material); Eocene: *Adapis, Pronycticebus, Necrolemur*; Miocene: *Progalago, Limnopithecus, Proconsul*; Pliocene: *Mesopithecus, Libypithecus, Pliopithecus*; Pleistocene: most of the Malagasy lemuroids and the African cercopithecids, the Chinese material of *Rhinopithecus*. For the Tertiary this makes a total of 10. Paleontology can speak with some authority on the taxonomy and phylogeny of certain of the living orders of mammals—for example, in Artiodactyla extinct genera outnumber living by nearly 4 to 1, in Perissodactyla by 25 to 1; it is evident, however, that it cannot yet do so for the Primates.

At this point, perhaps, the reader might reasonably expect the discussion to be concluded for lack of evidence. Things are not quite as bad as that, though. In any survey of a history it is very proper to

TABLE 1

Geological Record of Non-Hominid Primates in the Old World

TABLE 1

Geological Record of Non-Hominid Primates in the Old World

Divisions of Cenozoic Time and their estimated durations	PROSIMIANS														CATARRHINES								Genera Known in the Divisions of Cenozoic Time
	Tupaioids		Lemuroids					Lorisoids		Tarsioids					Cercopithecoids			Pongidae			Hominoids		
	Anaptomorphidae	Tupaiidae	Pleiadapidae	Adapidae	Lemuridae	Indridae	Daubentoniidae	Lorisinae	Galaginae	Microchoerinae	Anaptomorphidae	Tarsiidae	Apatemyidae	Proteinii, fam. inc. sed.	Cercopithecinae	Colobinae	Inc. Sed.	Inc. Sed.	Dryopithecinae	Hylobatinae	Ponginae	
Recent	:	5	:	:	6	3	1	4	2	:	:	1	:	:	10	6	:	:	:	:	3	43
Pleistocene L	:	:	:	:	6	6	:	:	:	:	:	:	:	:	1	:	:	:	:	2	1	14
M	:	:	:	:	:	:	:	:	:	:	:	:	:	:	2	1	:	:	:	:	1	6
1 million E	:	:	:	:	:	:	:	:	:	:	:	:	:	:	8	1	:	:	1*	:	1	11
Pliocene L	:	:	:	:	:	:	:	:	:	:	:	:	:	:	3	1	:	:	2	2	:	1
M	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	1	6
11 million E	:	:	:	:	:	:	:	1	:	:	:	:	:	:	:	1	:	:	7	1	:	11
Miocene L	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	2	1	:	3
M	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	2	1	:	3
16 million E	:	:	:	:	:	:	:	:	1	:	:	:	:	:	1	1	:	:	2	2	:	6
Oligocene L	1*	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	1
M	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	0
10 million E	1	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	4	:	1?	:	:	6
Eocene L	:	:	:	3	:	:	:	:	:	2	1	:	1	2(1*)	:	:	2	:	:	:	:	11
M	:	?	1	4	:	:	:	:	:	1	1	:	1	5	:	:	:	:	:	:	:	13
20 million E	:	:	1	1	:	:	:	:	:	1	:	:	1	:	:	:	:	:	:	:	:	4
Paleocene L	:	:	2	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	2
M	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	0
17 million E	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	0
Genera	2	5	4	4	10	6	1	5	3	3	2	1	2	7	16	8	6	1	9	5	3	103
Total	0	5	0	0	6	3	1	4	2	0	0	1	0	0	10	6	0	0	0	2	3	43
Living	2	0	4	4	4	3	0	1	1	3	2	0	2	7	6	2	6	1	9	3	0	60
Extinct																						

* Exact horizon doubtful.
? Systematic position uncertain.
N. B. A number of genera extend over more than one division of time.

state what the gaps are and where they occur, but it is equally proper to go on and do as well as possible with what is in hand. Every primate fossil is a precious relic that contributes its bit to the history of the order. True, the evidence thus far contributed is often capable of conflicting interpretations, but sooner or later matters iron out; new discoveries permit new perspectives, and progress, however halting, is made. Paleontology may not as yet be able to speak with authority, but it is now in a position to make suggestions that seem reasonable and worthy of attention. From here on, then, we can begin to look more at the positive, or brighter, side.

DISTRIBUTION

Some interesting data concerning geographical distribution are available. The scanty Pleistocene records show that the orang utan was in India during the Early Pleistocene, and thus suggest that it was present in south-eastern Asia throughout most if not all of the epoch. The few remains of Pleistocene gibbons extend the present range of *Hylobates* into southwestern China. Interglacial climates more favorable than the present permitted *Presbytis* to range westward into Europe and *Macaca* to extend as far north as England. *Papio*, together with *Macaca*, has been reported from the Mid Pliocene of India, but more complete remains would perhaps make a new generic assignment necessary. It is clear that, during the later Tertiary, the gibbon group ranged widely over the Old World, together with the rather heterogeneous and probably artificial assemblage known as the Dryopithecinae. The very few later Tertiary and the Pleistocene records of prosimians are all within the areas now occupied by their surviving relatives, a fact which supports the inference, reasonable on general grounds, that the Prosimii had by then been displaced by the catarrhine expansion, and relegated to the marginal areas or ecologic niches they now occupy. Our knowledge of earlier Tertiary prosimians is almost wholly limited to Western Europe, but we can be sure that the group was very wide spread in the Paleocene and Eocene. In general, as Cenozoic time went on, and Eurasia and Africa became progressively more unified, increasing opportunity for wide dispersal was available to successful groups.

The most important single zoogeographical datum in connection with primate history is this: since the Early Eocene, Old World and New World primate evolution appear to have gone their separate ways. We can state with confidence that some Paleocene primate exchange took

place between the hemispheres, witness the common presence of plesiadapids. *Plesiadapis* itself, by the way, is the only genus, other than *Homo*, known to occur in both. The lack of Early Eocene genera common to the two is surprising, because this was the time of greatest faunal interchange between Eurasia and North America, indicating a broadly open migration route (Simpson, '47). Primates surely participated in this interchange, but perhaps ecological barriers may have prevented their rapid spread westward in the Old World. The Early Eocene primate fauna of eastern Asia, if and when it is made known, may well turn out to be more similar to that of North America. So long as nothing is known east of Europe for this part of the Tertiary, it is of little use to speculate concerning the absence of various American super-generic groups in Europe. Suffice it to say that the general cast of the primate fauna, the degrees of evolutionary advance, etc., were broadly comparable in the two areas.

Following the Early Eocene connection, Eurasia and North America were apparently separated until the Late Eocene. Neither during this nor any of the later connections is there evidence of any primate migrations until *Homo sapiens* arrives on the scene. Conditions in the vicinity of the bridge, which was very probably in the Bering Strait region, were evidently unfavorable climatically for members of the order in existence at the various times of connection. This very early separation of the basal primate stock has a decided bearing on major taxonomy, as will appear.

SOME ASPECTS OF THE RECORD

Space is lacking for any detailed review of the factual evidence, and since nearly all of it has been so well described by authors whose works are thoroughly familiar, this is not too serious. I shall therefore take up only a few specific points and touch on one or two matters of general interest. The absence of any definite records of the Tupaiidae is puzzling, because, be they primates or only near-primates, they have certainly come down to us from the earliest times. It may perhaps be that we have them and do not know it. The tupaiid dentition is quite characteristic, but it is possible that this might have been acquired in post-Eocene time, with Eocene and Paleocene representatives consequently remaining undetected. The question mark in the Mid Eocene in table 1 refers to two genera recently referred to the family by Weitzel ('49). Unfortunately, his descriptions are cursory and given in general

terms, and he does not figure the tooth crowns. The general body form is quite tupaiid-like, but this by itself is hardly sufficient evidence. These forms may perhaps be related to the Paleocene adapisoricids and these in turn could conceivably be tupaioids, but this is all very conjectural.[1] The tupaioid affinities of the Anagalidae have recently been called in question. Bohlin ('51) has described *Anagalopsis* from a deposit in Central Asia that is not precisely dateable, but which may fall somewhere in the later Oligocene if we may judge from the dentition of this form, which is more advanced than that of *Anagale*. Advanced in a peculiar way, the teeth being sub-hypsodont and unilaterally so, in the manner of many rodents and some other forms. This is a decidedly odd feature for a primate, although not in itself grounds for excluding the family from the order. Bohlin regards the structure of the bulla, as he interprets it, as the decisive character. Since this has an open U-shaped cleft beneath the porus proper, and no meatus, he concludes that it must be formed by the tympanic, and not by the entotympanic as it is in tupaiids. It seems to me, however, that an entotympanic in the course of phylogeny might assume such a form, and I am therefore not yet prepared to throw overboard Simpson's careful evaluation of the evidence favoring inclusion of the anagalids in the tupaioids.

The whole Early Tertiary prosimian complex bristles with difficulties. Forms and series of forms are shuttled about from one division to another and there is disagreement over what should be included and excluded. For example, the microchoerids are placed by Gregory, Le Gros Clark, and Simpson in the Tarsioidea (by the last as a subfamily, Necrolemurinae, of Anaptomorphidae), while Hürzeler ('48), who has recently completed a careful study of them, believes that they are closer to the lemuroids and entitled to rank as a distinct superfamily. For some, the Apatemyidae are primates, for others not, and so on. Such disagreements among highly competent authorities, the conflicting evidence responsible for them, and the number of genera that cannot be definitely assigned, strongly suggest that the distinction between lemuroids and tarsioids was not at that time very profound (Simpson, '45; Barth, '50).

The mosaic of characters that makes classification of these forms so

[1] Following Teilhard de Chardin, the adapisoricids have been placed in the insectivore family Leptictidae by most authors. The early Eocene species referred to *Adapisorex* by Teilhard is a leptictid, but the type and other late Paleocene species do not appear to be referable to this family.

difficult may be traceable to conditions prevailing in the area during the early Tertiary. The reader will recall the changing relations between land and sea, the fluctuating climates, and the shifting vegetation zones that the geologic evidence seems to indicate. Note that the Paleocene and Eocene together make up almost exactly half of Tertiary time, if we can trust the present crude estimates of the duration of the epochs. Under such conditions and over such a length of time, small scale adaptive radiations would tend to arise in various separated regions. Reunion of these regions would lead to intergroup competition and to the reduction or elimination of the less well adapted of those groups that had happened to evolve in similar directions. Renewed separation would start the process anew. The genetic complex of any of these various stocks must have had much in common with those of all the others. Many mutations acting in these substrates would thus tend to have similar effects in distinct stocks, the closer the more nearly parallel the trends under way. As a result, not only would similar details of dental morphology be attained, but independently achieved characters would occur in the skull and post-cranial skeleton as well. The net result would be a confusing array of small groups, each one resembling the others in a variety of ways, a situation extremely difficult to deal with on the basis of fragmentary fossil material. A small sample from one region, such as we have from Western Europe or from Western North America, obviously will not permit us to reconstruct very much of the story. In fact, if paleontology succeeds in even partially unravelling the tangle it will be doing very well indeed.

At the end of the Eocene and the beginning of the Oligocene there appears a small array of genera—such as *Amphipithecus, Moeripithecus, Parapithecus, Propliopithecus, "Kansupithecus"* [2]—that was probably of the greatest importance in primate history. It is more likely than not that these forms arose from some anaptomorphid stock, and very possible that they, or rather the group they represent, were broadly ancestral to the Hominoidea and to the Cercopithecoidea. It is therefore the more unfortunate that our knowledge of them is confined to the lower jaw. One, *Propliopithecus*, has been hailed as an ancestral gibbon; it might about equally well, perhaps, be regarded as standing somewhere in the line of the Hominoidea as a whole (the others occur in the table under Catarrhini *incertae sedis*). It is at this point in history, just

[2] This name is technically invalid, Bohlin ('46) having failed to name a species.

when things are getting really exciting, that the curtain descends on the higher primates, to remain down for two full subepochs. When it rises again in the Early Miocene, we are presented, thanks to the magnificent discoveries in East Africa, with an undoubted cercopithecid, generalized pongids and a primitive gibbon.

Taking up the Cercopithecidae first, what strikes the eye is that the colobines have, in the books at least, a longer recorded history than the cercopithecines. This is based on *Mesopithecus*, known from the Early Pliocene, to which the Early Miocene East African form has been tentatively referred in preliminary notices. There is something a little puzzling here. The living colobines tend to be rather strictly arboreal, and their diet, as is well known, consists largely of leaves, for the digestion of which they have a specialized stomach. *Mesopithecus* is probably the most completely known fossil primate and its remains are quite common in Pontian deposits, skulls having been found in groups (Abel '27, p. 133). The associated fauna is that of a steppe region, horses, antelopes and other open country forms occurring in numbers. If *Mesopithecus* was a colobine with the diet and habitat preferences of its living relatives, why is it so common in a steppe fauna? A form living in trees along watercourses, as *Colobus* does in East Africa today, would hardly leave skulls in groups. A reexamination of the affinities of *Mesopithecus* would seem in order; the field evidence suggests cercopithecine relationships. The remaining cercopithecids call for no comment in a review of this brevity.

The case of *Oreopithecus*, frequently considered to be a cercopithecid, deserves passing mention, if only as a horrible example of what should not happen. Originally described in the 1870's, a literature of approximately 80 papers has grown up around it. Three views as to affinities have been held: that it was a pongid, an aberrant cercopithecid, or a sort of connecting link between the two. Hürzeler ('49) has recently made a thorough restudy of the genus and has concluded that it is a pongid ("anthropomorph") of uncertain affinities, and has nothing to do with the Cercopithecidae. It is shown in the table in the Early Pliocene under Pongidae *incertae sedis*. Now comes the depressing part of the story. Hürzeler believes that only 11 of the many papers describing or referring to the animal were written by authors who had seen original material. The others were based on the previous literature, on the published figures, or on some casts that appear to have been widely distributed. The figures were inaccurate and the casts were

misleading. Schwalbe, author of the longest and most quoted paper, apparently worked from the casts. Gregory, also working from the casts and laboring under the misapprehension that the age was Early Miocene, thought he detected a resemblance between *Oreopithecus* and the problematical *Apidium,* and from this stems the view that *Apidium* might have had something to do with the ancestry of the cercopithecids. Students of the fossil hominids must all be familiar with situations of this sort, expenditures of time and energy that resulted only in confusing the issue. This and similar cases should inspire us to take steps to insure that such does not occur again. Of this more anon.

On dental evidence, the gibbons can be traced back to the Early Miocene, certainly, and perhaps on back to *Propliopithecus.* Of the Ponginae, neither *Pan* nor *Gorilla* has a fossil record. *Pongo* is recorded from teeth throughout the Pleistocene, and Hooijer ('51) has recently discussed a Mid Pliocene P_3 from the Siwaliks, which he finds indistinguishable from that of the living species. The bulk of the pongid records is of course formed by the Dryopithecinae. The relatively numerous Late Miocene and Pliocene finds are unfortunately not very helpful in tracing lines of descent, but they do show that a fairly rich variety of hominids was then in existence. The magnificent finds of *Proconsul* are so familiar that there is no need to go into any detail here. It is enough to say they reveal that an Early Miocene pongid had a brain of generalized catarrhine type, a jaw that had relatively narrow incisors and lacked a simian shelf, and limb bones that were not specialized for brachiation. Presumably it progressed to a considerable extent on all fours. The contemporary gibbon *Limnopithecus,* the Pliocene gibbon *Pliopithecus* (Zapfe, '52), and such few skeletal fragments of later dryopithecines as we have, combine to suggest that a similar body form, at least, was characteristic of Miocene and earlier Pliocene pongids generally.

SOME POSSIBLE INTERPRETATIONS

So much for this very brief and necessarily incomplete survey of the available facts. A body of data requires organization if it is to have meaning, and paleontological data are perhaps most succinctly expressed in the form of phylogenetic diagrams. The fact that such diagrams are notorious for the wide difference of opinion they usually display does not detract from their usefulness as shorthand expressions of different viewpoints. The scheme shown in figure 2 was published

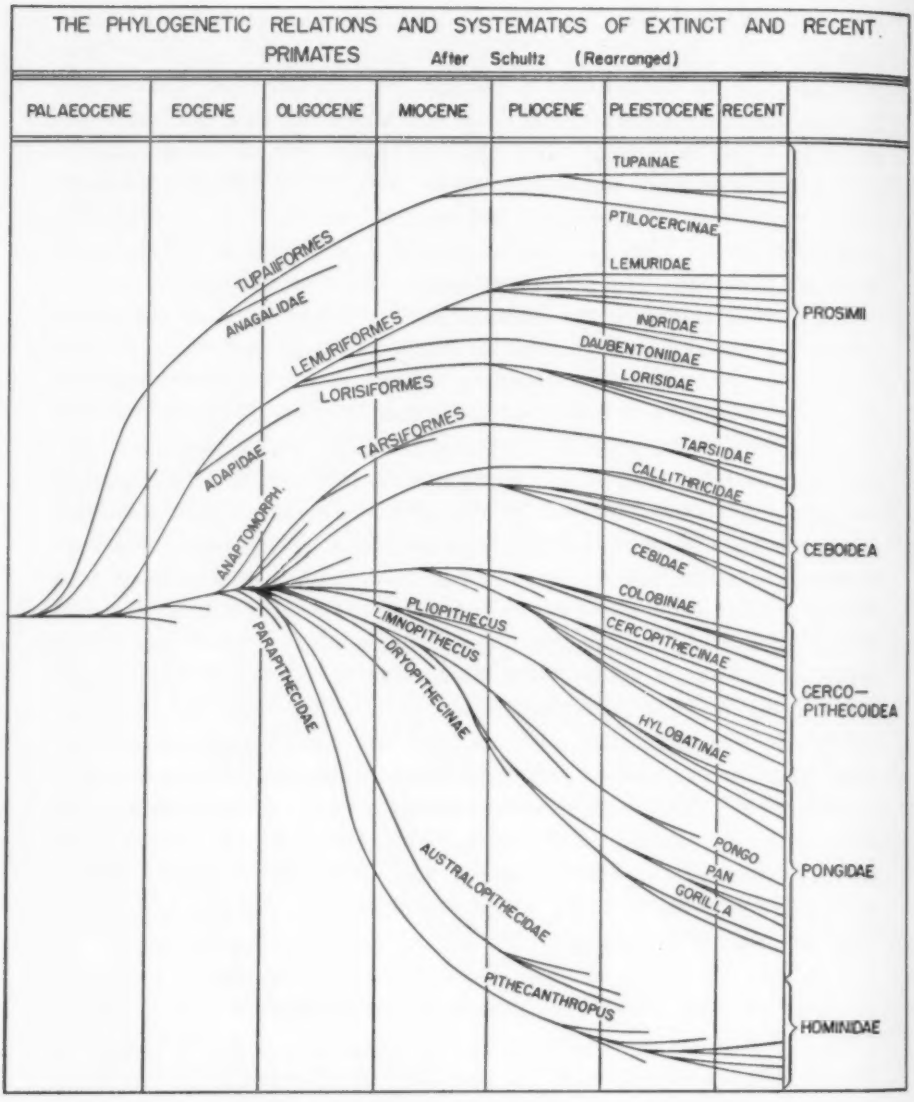


FIG. 2. ONE VIEW OF PRIMATE PHYLOGENY. AFTER SCHULTZ, REARRANGED.

recently by Adolph H. Schultz ('53), one of the great students of Recent primates. It contains some questionable features. To begin with, some of the lines appear to be split unnecessarily far back. I find it incredible that the Hominidae should have originated at the beginning of the Oligocene, or that the *Australopithecus* group should have parted company with them shortly thereafter. The *Pan* and *Gorilla* lines surely were not separate in the Early Pliocene, and it is perhaps doubtful if the *Pan-Gorilla* and *Pongo* phyla go back as far as the Mid Miocene. On the other hand, the break-up of the Cebidae certainly took place long before the Pliocene. Going on to more general topics, it is misleading to represent all extinct groups as so many minor twigs from main branches that extend without deviation or interruption from the distant past to the present, and the depiction of a main trunk running from Paleocene almost to Oligocene is somewhat of an oversimplification. Schultz's diagram has not been singled out merely for the sake of captious criticism, but because I suspect that it is a rather representative example of how primate evolution may appear to those who look into time from the vantage point of the Recent.

Figure 3 is submitted as an example of how the picture appears to one who tends to look into time from the opposite direction.[3] Viewed in this light, primate history has the appearance of a succession of radiations of varying scope.

The dashed lines at the base of the figure are not there for purely decorative purposes. As Professor Jepsen remarked in the course of the Symposium, only three living orders, one of them non-placental, have a longer recorded history than the primates. A character fundamental to the evolution of the Theria was the acquisition of the so-called tribosphenic molar, from which the primate and all other types have been derived. It is now known that this molar type had come into existence by the middle of the Cretaceous Period. During that part of the Age of Reptiles represented by the Late Cretaceous—a long stretch of time, probably longer than the Eocene, for example—mammals must have undergone a considerable amount of diversification. At present,

[3] Those familiar with the scheme presented by Simpson in his *The Meaning of Evolution* ('49, fig. 17, p. 91) will note a considerable degree of resemblance. The two are actually independent. The explanation for this lies in the fact that Simpson's book exists in two editions. In one, which I read, presentation and discussion of factual evidence is abbreviated, and the figure in question is not included. I did not see it in the first edition until after figure 3 had been drafted. The agreement between the two is encouraging.

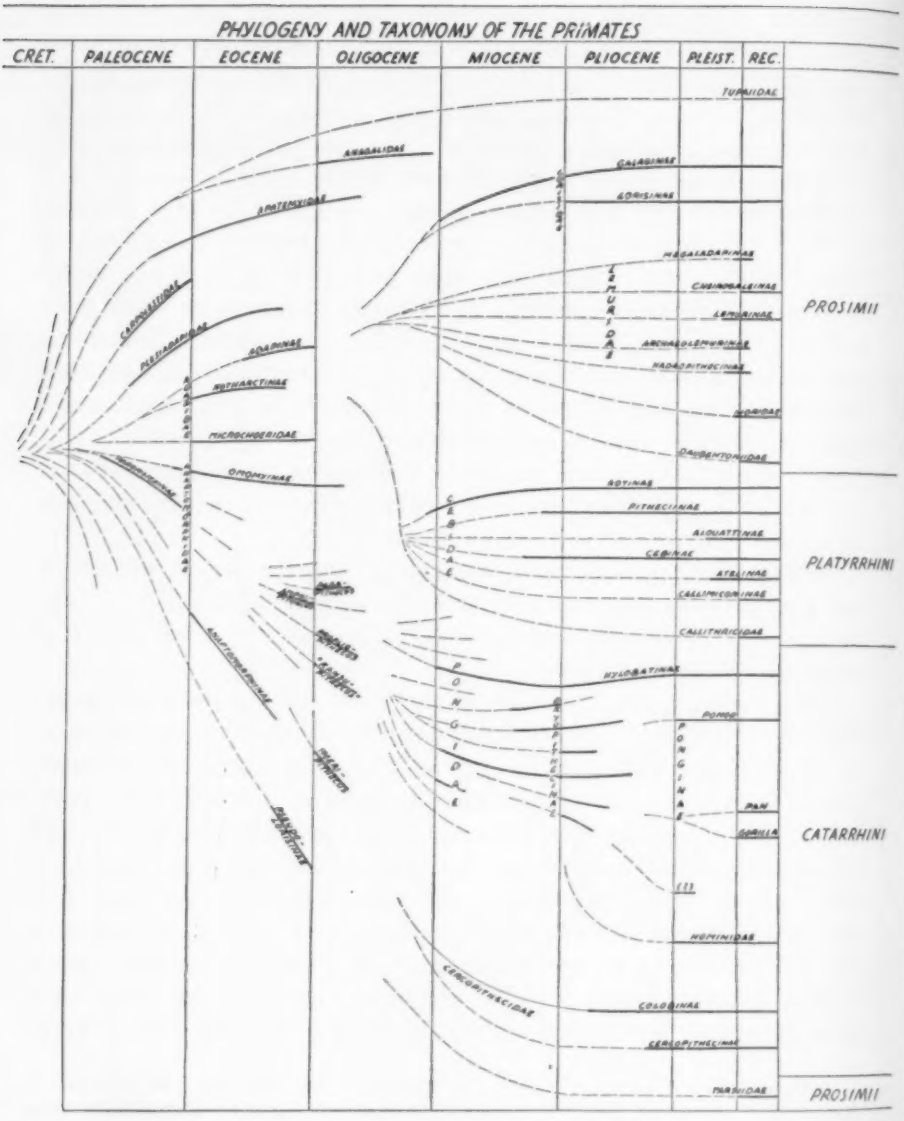


FIG. 3. ANOTHER VIEW OF PRIMATE PHYLOGENY. KNOWN RANGES ARE SHOWN IN SOLID LINES, STARTING WITH THE EARLIEST FORMS THAT CAN BE REFERRED WITH ASSURANCE TO A PARTICULAR GROUP.

we know next to nothing about this earliest therian radiation, but we can infer that it took place—the diversified mammals of the Early Paleocene certainly did not come into existence overnight. "Proto-primates" and "para-primates" surely formed part of it. Tupaioids, macroscelidids, perhaps apatemyids may have appeared at about this time, together with such poorly known groups as the adapisoricids and metacodontids.[4]

Out of this radiation, possibly even a part of it, came the prosimian complex of the Paleocene and Eocene. If the dentition is any guide, these forms were a highly diversified lot, and it is possible, as Barth has suggested, that they were not all arboreal but may have filled a number of ecologic niches open to small mammals, particularly in Paleocene and earlier Eocene time. This prosimian radiation seems to have largely ended with the Eocene, at least in regions from which we have reasonably good fossil records. The rise of modern types of rodents and of carnivores, which occurred about this time, may have been a contributing factor, but more important, probably, was the rise of the catarrhines. Tupaiids, lorisids, and tarsiids have managed to survive the catarrhine inundation, but only by adaptation to ecologic niches in which they have escaped from competition. The only later Cenozoic prosimian expansion, that of the lemuroids, is the result of an accident. African prosimians, perhaps adapines, reached Madagascar (a region to which no non-hominid catarrhine, and indeed few mammals of any sort, ever penetrated), possibly in Oligocene time and certainly by overseas transport, and there gave rise to the profusion of Recent and Late Pleistocene forms for which the island is so justly famous.

A point to be made here is that the Paleocene and Eocene forms, not the terminal twigs that survive today, were the "real" Prosimii. As noted, the early forms have much in common structurally, and constitute a reasonably compact group. As regards taxonomy, I would heartily agree with Simpson that it is preferable to include all, both early and late, in one suborder.

If I may be pardoned a digression into the New World, the platyrrhine radiation, like the lemuroid, was also the result of an accident of dispersal, this time from North America. The South American fossil record permits the assumption that the date was in the first half of the Oligocene. As Gregory has suggested, the ancestral forms may possibly

[4] The last, a North American group, may be represented in the European Eocene by *"Adapisorex" anglicus* Forster Cooper.

have been notharctines, but this is very uncertain. A peculiar fact concerning the platyrrhines is that we have no good evidence that they ever evolved predominantly ground living types, despite the fact that the general situation, absence of placental carnivores, etc., would seem to have been more favorable in South America than in the Old World. This appears to be one more instance showing that the existence of an evolutionary opportunity does not insure that it will be seized. In figure 3, the lines of descent of the various ceboid sub-groups are projected very nearly to the presumed date of ingress. Theory and an excellent example from another order may be cited in support. As Wright ('49, p. 387) has remarked: "When . . . unoccupied territory is reached, a very extensive and rapid adaptive radiation should follow under the divergent selection pressures toward exploitation of the various special ecological niches, opened up by . . . the mere absence of competition . . ." The caviomorph rodents, whose ancestors reached South America by accidental means at about the same time as those of the platyrrhines, illustrate this perfectly, their major subdivisions becoming established almost from the start.

The fact that South American primates had an ancestry distinct from that of the catarrhines since at least the Early Eocene, taken together with their morphological peculiarities, entitles them, I believe, to subordinal rank. Retention of the time-honored terms Platyrrhini and Catarrhini would appear to be justified.

The catarrhine radiation, the most important from our point of view, began before the end of the Eocene. Beyond this important fact we know almost nothing, due to the fragmentary nature of the few known Late Eocene and Early Oligocene specimens and the lack of any records from the Middle and Late Oligocene. The cercopithecoid-hominoid dichotomy occurred before the Miocene but just when we do not know. Very successful in their own sphere, cercopithecoids clearly had nothing to do with the ancestry of any other catarrhine group, and need no further consideration here.

In reading the descriptions and discussions of the Miocene hominids, it is possible to detect here and there a note of surprise concerning the evidence that they seem to have possessed a quadrupedal gait. The catarrhine radiation was a fairly late one, geologically speaking; the ancestral forms were certainly quadrupedal, and it is therefore not too remarkable that the earlier hominoids should also have been to an extent quadrupedal or that some, at least, remained so into Pliocene time.

The new discoveries in fact deal a death blow to some old arguments concerning the origin of man, arguments which appear to have stemmed from typological thinking. Gibbons have rather distinctive molars, and because of this it is possible to trace a phyletic thread back from the present that does not get lost in the dryopithecine tangle. The Early Oligocene *Propliopithecus* could on this evidence be an ancestral gibbon, and has often been so regarded. As a result, a train of reasoning something like this appears to have prevailed in some quarters: living gibbons are brachiators par excellence; *Propliopithecus* was a gibbon, ergo it was an excellent brachiator; the ancestral pongines must have been too; man does not brachiate, ergo his ancestors must have branched off before this adaptation became established; *Propliopithecus* is Early Oligocene in age, ergo the Hominidae arose in the Eocene; Q. E. D. The new evidence, which rather strongly suggests that extreme specializations in locomotion occurred quite late in hominoid history, does away with this old objection to close affinity between hominids and pongids. Proponents of this affinity no longer have to combat the contention that a radical change in the direction of adaptation would be necessary in order to derive the one from the other. The concept responsible, basically, for the old arguments against such derivation was the notion, once rather prevalent, that all parts of animals evolved at about the same rates, a view repeatedly shown to be erroneous.

The generalized locomotor apparatus of later Tertiary hominoids has been hailed as showing that man's ancestry did not pass through a brachiating stage, hailed almost with relief, as though brachiating were some deadly sin. I submit that this is going too far and that there is no real evidence for it. The objections to such a stage perhaps stem in part from old views and may also be in part semantic—the word brachiation being associated with the extreme conditions in living pongids. There would seem to be nothing in the known structure of the earlier pongids to indicate that they did not brachiate to some extent, and, as Gregory has long insisted, a moderate amount of brachiation seems to be the best explanation of how the hominid line got up on its hind legs. Our ancestors, however, unlike those of the living pongids, were able to take their brachiation or leave it alone. The extreme degree of this adaptation shown by hylobatines and pongines today may be as recent an event in primate history as acquisition of the upright gait.

Some recent authors who favor an origin of the human stock from

the pongid, branch us off in the Early Miocene, if not earlier, again perhaps in an effort to avoid the demon brachiation. In figure 3, this event is postulated to have occurred considerably later. In view of the rapid evolutionary progress made by the hominid line during the Pleistocene, there seems to be no compelling reason for assuming that the earlier stages should have required longer than the 10 million years or so allotted to the Pliocene. Man is the result of an adaptive shift in the direction of evolution, and such events are rapid, geologically speaking. But man is a non-non-hominid primate and I must not discuss him further.

These are the ideas of one paleontologist concerning the reasonable suggestions that paleontology can make about primate history (novelty for any of them is, of course, disclaimed). They are as tentative as our story is incomplete, but the history of primate discovery holds forth the promise of a far better base on which to build. Vertebrate paleontology is roughly 150 years old. By the end of the first third of this period, say up to 1859, only 7 extinct genera of primates had been described. Between 1860 and 1900, 21 more were added (these figures are for the world); between 1901 and 1925, 33 and since 1926, 46. If this can be kept up, we should be well off some day, but in the meantime we are not getting the most out of what we have. Professor Straus recently remarked that it would be nice if good casts of the australopithecines were generally available. I should like to go further and say that casts or photographs of all important fossil primate specimens should be prepared and made widely available for exchange or purchase. With existing media, especially latex, magnificent casts can be made. Stereoscopic photomicrographs from various aspects would serve for small and delicate specimens. This sounds like an ambitious program, but it seems a good way to avoid more *Oreopithecus* incidents. If, then, we can continue the rate of discovery and provide for wide use of the materials we have and hope to get, our grandchildren will perhaps have the beginnings of a workable outline of primate phylogeny, and on this properly qualified note of optimism this brief presentation may be closed.

LITERATURE CITED

ABEL, O. 1927 Lebensbilder aus der Tierwelt der Vorzeit. Gustav Fischer, Jena.

BARTH, F. 1950 On the relationships of early primates. Am. J. Phys. Anthrop., n. s. *8*: 139-149.

BOHLIN, B. 1946 The fossil mammals from the Tertiary of Tabun-buluk. Rept. Sino-Swed. Scient. Exped. N. W. Prov. China. *6*: no. 4.

——— 1951 Some mammalian remains from Shih-ehr-ma-ch'eng, Hui-hui-p'u area, western Kansu. Ibid. no. 5.

HOOIJER, D. A. 1951 Questions relating to a new large anthropoid ape from the Mio-Pliocene of the Siwaliks. Am. J. Phys. Anthrop., n. s. *9*: 79-94.

HÜRZELER, J. 1948 Zur Stammesgeschichte der Necrolemuriden. Schweiz. Pal. Abhandl. *66* (3): 1-46.

——— 1949 Neubeschreibung von *Oreopithecus bambolii* Gervais. Ibid. *66* (5): 1-20.

——— 1949 Über die europäischen Apatemyiden. Verh. Schweiz. Naturf. Ges. *129*: 140-141.

SCHULTZ, A. H. 1953 Man's place among the primates. Man, *53*: 7.

SIMPSON, G. G. 1945 The principles of classification and a classification of mammals. Ibid., *85*: 1-350.

——— 1947 Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. Am. *58*: 613-687.

——— 1949 The Meaning of Evolution. Yale Univ. Press, New Haven.

TEILHARD DE CHARDIN, P. 1916-1922 Les mammifères de l'éocène inférieur et leurs gisements. Ann. Paleont. Paris. *10*: 171-176; *11*: 1-116.

WEITZEL, K. 1949 Neue Wirbeltiere (Rodentia, Insectivora, Testudinata) aus dem Mitteleozän von Mersel bei Darmstadt. Abh. Senckenb. naturf. Ges. no. 489, 1-24.

WRIGHT, S. 1949 Adaptation and selection. *In* Genetics, Paleontology and Evolution. Princeton Univ. Press, Princeton, N. J., pp. 365-389.

ZAPFE, H. 1952 Die Pliopithecus-Funde aus der Spaltenfüllung von Neudorf an der March. CSR, Verh. Geol. Bunlesanst., Wien. Sonderheft C: 126-130.

COMPARATIVE ANATOMY OF NEW WORLD PRIMATES AND ITS BEARING ON THE PHYLOGENY OF ANTHROPOID APES AND MEN

(ABSTRACT)

BY G. E. ERIKSON

Harvard Medical School
Boston, Massachusetts

THE platyrrhine primates, long slighted as a side issue in the study of human evolution, have a peculiar relevance to that study by virtue of this very isolation. Independently evolved from Eocene lemuroids or tarsioids, the New World monkeys have developed a remarkable series of features closely paralleling those developed in the Old World radiation. The aspects of this parallelism most significant for the study of the evolution of anthropoid apes and men are those related to their locomotion and posture. In addition to the platyrrhine counterpart of the catarrhine monkey, the New World radiation produced three genera (*Ateles*, *Brachyteles*, and *Lagothrix*) capable of brachiation and displaying certain adaptations to upright posture.

A comparison of the structural correlates of brachiation in Old World and New World primates provides a revealing technique in attempting to distinguish genetic from adaptive resemblance in closely related living forms and aids in the reconstruction of form and function in fossil relatives. In the present study a more precise definition of brachiation has been sought and contrasts have been made with typical arboreal quadrupedal locomotion and terrestrial bipedalism. This involves an analysis of the proportionate lengths of limbs and their segments and a comparison with trunk lengths, the proportions and articulations of the thoracic and lumbar spine regions, and the adaptive mechanisms in the musculo-skeletal structure of shoulder and hand.

A full appreciation of the significance of this parallelism must await further study of these little known primates.

PRIMATE EVOLUTION FROM THE VIEWPOINT OF COMPARATIVE ANATOMY

BY D. DWIGHT DAVIS

Curator of Vertebrate Anatomy
Chicago Natural History Museum

PHYSICAL anthropology, in so far as it deals with comparisons of the structure of the primates, is a branch of comparative anatomy. The goals, the limitations, and the methodology are then those of comparative anatomy. It may therefore be profitable to consider physical anthropology against the broader background of comparative anatomy, to see whether it has kept pace with development in the parent field.

I am not an anthropologist, and I therefore have no anthropological tradition to prejudice my views. The fact that I am not an anthropologist also implies, of course, that I am grossly ignorant of the details of this science. In this review we are not interested in details, however, but in general principles—which may easily become blurred or even obscured if we are too much preoccupied with details.

Let us begin by considering very briefly the history of comparative anatomy, since changing fashions in comparative anatomy would be reflected in interpretations of primate evolution.

THE EVOLUTION OF COMPARATIVE ANATOMY

Comparative anatomy is one of the oldest scientific disciplines, and its aims and concepts have undergone considerable changes. These were not random changes in direction. On the contrary, they follow a definite pattern. In part they reflect the evolution of general scientific concepts, and in part the growth of morphological knowledge itself. No real understanding of comparative anatomy is possible unless these shifts in purpose are appreciated.

Until the middle of the nineteenth century the goal of comparative

anatomy was to discover the several "ideal plans" that were believed to underlie the structure of organisms. It is difficult to appreciate the viewpoint of this by-gone era, when the concepts of historical change and blood relationship between species had not yet entered biological thinking. The ideal plans were formal abstractions, devoid of meaning to their discoverers, except to those devout Christians to whom they represented the master blueprints of the Creator. Linnaeus, when he placed man in his order Primates, certainly was not thinking in terms of blood relationship. Like the structure of crystals, or the periodic table of the elements (as then understood), the common plans represented only ordered systems. This concept is best seen in the works of Cuvier and others of the eighteenth and early nineteenth centuries. This period in the evolution of comparative anatomy produced an immense body of factual data that was incorporated into the period that followed. Its most important achievement was the concept of homology and analogy, developed by Owen, which is still the basic tool of comparative anatomy.

Looking back from the vantage point of today, it is incredible that the simple and obvious interpretation was not seen—that common structure is a product of common ancestry. Yet the history of science shows that such mental blocks are not uncommon; we need recall only the equally remarkable history of the phlogiston theory, which held thinking in chemistry and physics enthralled for centuries.

The dramatic shift in the goal of comparative anatomy immediately following the publication of the *Origin of Species* in 1859 is too well known to need more than passing mention. Almost overnight, once the idea of descent with modification was grasped, comparative anatomy was completely re-oriented. The goal then became to discover the history of the structural elements of the animal body, and thus of the organisms themselves; in other words, the portrayal of the true course of phylogeny. *This is the theme of every textbook of comparative anatomy in use today, and the motivation of nearly all research in this field.*

This is a sterile aim. Classical comparative anatomy has never gone beyond inferring and describing the temporal sequence of biological events, and this is merely systematized knowledge. Dr. James B. Conant recently contended that systematized knowledge does not of itself constitute a science, that such knowledge is significant only as it gives rise to new ideas or concepts. This seems to me to be a valid criterion, and it is precisely at this point that classical comparative anatomy failed. If the concepts of Gegenbaur, Wiedersheim, and their spiritual descen-

dants are the final chapter in the evolution of comparative anatomy, then this science deserves all the hard things that have been said about it. The central problem of historical biology is to explain, not to describe, the historical events that produced the bewildering diversity of living organisms that inhabit the earth today.

Essentially all modern biologists have abandoned belief in any of the mystical drives that have been suggested as forces in evolution. The evidence is overwhelming that evolution is non-purposive and non-directed, that it is opportunistic, based on probabilities. At every stage in a given lineage alternative courses were open and the one actually followed was determined in each instance by the interplay of random genetic factors in the breeding population on the one hand, and the complex of factors in the environment on the other. The factors that determined shifts in adaptive direction may have been, and probably usually were, very trivial at the outset, however far-reaching their ultimate results. Each lineage is thus the result of a continuous but constantly changing complex of probabilities, an organism-environment relationship so precariously balanced as to suggest that evolution is truly indeterminate, that if the whole show could be run off again the outcome would not be the same, and might indeed be very different.

On such an indeterminate view, phylogeny is merely a pattern of what *did* happen in one particular case, merely one of an enormous number of possible patterns that could have resulted under identical circumstances. Phylogeny looks orderly and purposive, like the unfolding that the word "evolution" implies, but actually it looks purposive only in retrospect. Past events determine future events in evolution, not directly and absolutely, but only by altering future probabilities. The difficult problem of discovering how this enormous complex of shifting probabilities works can be solved only by analyzing how it did work in a great many cases. William Wightman, in his recent book *The Growth of Scientific Ideas*, called form, the subject matter of comparative anatomy, "a plastic record of the history of organisms." The broad goal of comparative anatomy should be, I believe, to attempt to interpret the why of this plastic record by considering it against the factors that are known to determine form. This includes pertinent data from genetics, experimental embryology, paleontology, ecology—a synthesis, in short, of all biological data that bear on the question of form. In less ambitious projects—the phylogeny of man or of a species of bear, for example—the principle is still the same; it is more important to know

why a particular direction of evolution was followed than merely to know the direction.

This involves a considerable re-orientation of the aims and methods of comparative anatomy.

THE NEW COMPARATIVE ANATOMY

Two ideas have deeply affected the recent thinking of comparative anatomists. Neither was a product of morphological research. The first was the suggestion, made originally by Goldschmidt ('27), that the timing and rates of developmental processes are gene-controlled. This provided a mechanism whereby individual genes, by controlling patterns of differentiation and growth, may affect whole morphological units, in addition to the genes that control the individual " characters " with which the experimentalist is usually concerned. This kind of gene effect is difficult to demonstrate experimentally, because changes in early morphogenetic processes usually have lethal consequences. It has been established by a considerable body of evidence, however, both experimental and observational. I reviewed the subject briefly elsewhere (Davis, '49). I believe that the importance of this concept to comparative anatomy cannot be exaggerated.

Each of the major taxonomic categories represents an adaptation to a particular way of life, to exploiting a particular ecological opportunity. The phyletic evolution of such an adaptive type is relatively easy to understand; it is the *origin* of major adaptations that presents difficulties. In most cases the major adaptation is quite obvious: the bats for flight, the carnivores for predation, the whales for swimming. Even at lower taxonomic levels the adaptive relations are often clear-cut: the vampire bats for blood-lapping, the nectar-feeding bats for extracting nectar from flowers; the dogs for running down their prey in packs, the cats for pursuing theirs alone and by stealth. It is remarkable—and unfortunate from our standpoint—that the primates, almost alone among the large and successful orders of mammals, are not characterized by an obvious and clear-cut major adaptation.

The second idea was the morphogenetic field concept, which is a corollary of the first. The morphogenetic field concept makes it possible, in many cases at least, to reconstruct the history of the genetic changes that underlie major adaptations. If such major morphological units as the whole molar toothrow, the whole thoracolumbar section of the verte-

bral column, or the whole masticatory musculature, are each subject to some sort of unitary control in addition to the detailed gene-character relations familiar to experimentalists, then the building blocks of evolution may be enormously simplified. Techniques can be developed for detecting morphogenetic fields where they cannot be delimited experimentally, and phylogenetic changes in terms of these units can be traced. If shifts in adaptive direction frequently involved such units as this, I believe we are, as morphologists, little concerned with the minor polishing of the basic adaptations, or with the mere multiplication of "characters" that is usually involved in speciation. The important, decisive events are the ones that set the stage for exploiting new ecological opportunities. Apparently they often have "trigger" or "threshold" effects that under favorable conditions may result in a period of explosive evolution. They also, of course, restrict and delimit the future possibilities of the lineage. An important aspect of such phenomena is that they can be seen to be preadaptive only in the light of subsequent events. At the outset of a new adaptive relationship the possible workable organism-environment relationships are so numerous and depend so heavily on chance, and the factors initially tipping the balance in a given direction are often so trivial, that prediction is impossible.

Statisticians point out that generalized effects would be far less likely to become established in a breeding population than would accumulations of many small deviations screened by natural selection. Relatively major phenotypic effects have therefore been practically dismissed from consideration as a factor in evolution. There is considerable evidence, which seems to me incontrovertible, that such effects did play a part, and I don't see how it can be ignored.

This dynamic approach to comparative anatomy has scarcely been tried. It is much more difficult and tedious than the familiar study of phylogeny. It involves techniques and disciplines that are unfamiliar to anatomists. The results, however, are vastly more rewarding.

THE METHOD

It has long been customary to recognize two distinct elements in the morphology of an organism: the "heritage" characters inherited from its ancestors, and the "habitus" characters that are correlated with its particular way of life. This simple dichotomy can be expanded into a hierarchy in which the habitus characters of yesterday become the heritage characters of today. For example, some of the heritage charac-

ters of the Hominidae obviously were the habitus characters of the common ancestor of the superfamily Hominoidea, in which they represented the new major adaptation of the man-anthropoid ape stock. Some of the heritage characters of the Hominoidea, in turn, were the habitus characters of the common ancestor of the suborder Anthropoidea, and so on back to the habitus characters (the basic vertebrate adaptation) of the subphylum Vertebrata, and even beyond.

This sorting of the new from the old is basic to any understanding of the morphology of an organism. It is, of course, the basis for our system of classification. It warns us, for example, that the closed orbits, the molar structure, the opposable thumb, and many other features of man are not strictly human characteristics. This warning is often unheeded in practice, and attempts are made to interpret the anatomy of an organism as if an engineer had designed it from scratch, specifying materials and sub-assemblies purely on the basis of functional requirements.

I regard this sorting as the first step in deciphering the mechanism whereby a given terminal condition was achieved in evolution. It separates out those conditions that represent earlier adaptations inherited from a long line of ancestors. This step might be formulated as:

(1) *In what respect does the morphology of the species or group under consideration differ from the next more generalized condition?*

This step involves straight comparison of form, the familiar procedure of classical comparative anatomy. It is at this point that classical comparative anatomy stops. But this is only a first step, because it is only those features that are directly subjected to selection pressures that are significant in adaptation. Among the numerous differences we have segregated in our first sorting there are almost certainly some not directly related to the new functional requirements. These may be merely indifferent. In snakes, for example, the anal plate may be either single or divided in closely related genera, and it is difficult to conceive of any functional significance in this. The exact tail length of many short-tailed mammals very probably has no relation to habits. There are also secondary adjustments resulting from functionally important changes in adjoining parts. For example, I have studied mammals in which the orbit is depressed far below its normal position, producing remarkable alterations in the Frankfort plane. These were forms in which the temporal muscle was enormously enlarged, however, and it was the expansion

of this muscle that crowded the orbit downward, not an adaptation involving the eye. Finally, there may be differences without functional significance that result from a genetic tie-up with another structure that is functionally important.

It is, of course, impossible to prove that a given condition is not related in some obscure way to the functional requirements of the animal. Careful attention to architecture and engineering, and above all detailed knowledge of the habits and behavior of the animal will, however, often reduce the probability almost to zero.

The second step may be formulated:

(2) *Which of the observed differences are directly related to the different functional requirements of the derived form?*

The functionally important features we have now isolated still are not limited to those under direct genetic control. Many morphological features, although functionally of the greatest importance, are only developmental consequences of other features that are under direct genetic control. In the absence of the primary structure such secondary features fail to appear. They may be described as "genetically determined once removed," since in the end their appearance or non-appearance does depend on genetic factors. The surface modelling on bones, for example, is determined by muscles and tendons rather than by genes acting directly on the bones, and most of the detailed architecture of bones is a non-genetic response to stresses and strains. When endocrine actions are involved, as in the enlarged sagittal crest of the male gorilla, the genetic basis for hypertrophy of the crests may be twice removed. In all cases, of course, the range of response is not unlimited, and is presumably genetically controlled. That a particular feature of a structure is not under direct genetic control can be determined by observation, but only experimentation can prove that a feature is genetically controlled. Without experimentation genetic control can only be inferred.

The third step may be formulated:

(3) *Of the differences directly related to new functional requirements, which are under direct genetic control and which are merely developmental consequences secondarily related to the genetic substrate?*

The fact that a functional element is under direct genetic control does not of itself guarantee that selection acting on the element is responsible for the observed condition of the element. Development of

a structure may, for example, be achieved via a differential growth rate. The growth pattern may have produced a close adaptive relationship at the time it was introduced. But if subsequent selection is for increased organism size, then the special structure will, because of its exponential growth rate, increase in size and/or complexity at a faster (or slower) rate than the entire organism. With increasing size, selection will usually be increasingly negative for the special structure, until an equilibrium between this negative selection and positive selection for total organism size is reached, or until the organism reaches the optimum size limits set by other factors.

Exponential growth rates by their very nature tend to produce developments so spectacular that they seem to demand functional explanations. Yet we know that the enormous antlers of moose and of the extinct Irish elk have gone beyond the stage of maximal usefulness. I find that the development of the dentition of the huge cave bear fits into an exponential curve based on skull size. I suspect that the grotesque nose of the male proboscis monkey (*Nasalis*) has a similar basis rather than representing a product of sexual selection. Developments such as these may have no positive relation to the requirements of the animal, however conspicuous and characteristic their form may be. Their genetic roots may lie far back in the ancestry of the organism we are studying.

Having localized in the morphology of our sample those features that represent the primary results of natural selection, the adaptive features resulting from the interplay of a particular environment and a particular genetic substrate, what can we do with them? I find that in the Carnivora the number of such features remaining after the final sorting may be surprisingly small, perhaps as few as half a dozen. We probably never will know the exact genetic mechanism behind such adaptive specializations, although in favorable cases even this can be inferred. At the very least we have localized the important elements of the evolutionary mechanism that were involved in a specific case. At best we have shifted our viewpoint from a comparison of static structure to the dynamic processes that determine structure.

Finally, the morphology of an organism cannot be interpreted except in the light of all of its antecedents. Any phyletic line represents a succession of adaptive relations. Earlier adaptations, particularly the morphogenetic processes whereby they were achieved, may have the most profound and unexpected repercussions many generations and many

adaptive relations later. If as a non-anthropologist I may venture a suggestion as to what seems to me the most desirable step in attempting to understand the evolution of man, I would recommend studying the treeshrews—and even the generalized insectivores. To me it is incredible that these creatures, in which the decisive steps leading to man may already have been taken, are almost unknown while we continue to lavish our attention on the higher primates.

Knowledge of structure without corresponding knowledge of function is sterile, and I should like to see a project, similar in scope to Carpenter's ('34; '40) work on the gibbons and howling monkeys, set up to study the habits and behavior of the Tupaiidae.

LITERATURE CITED

CARPENTER, C. R. 1934 A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). Comp. Psychol. Monog., *10*: 1-168.

——— 1940 A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). Comp. Psychol. Monog., *16*: no. 5, 1-212, 30 pl.

DAVIS, D. D. 1949 Comparative anatomy and the evolution of vertebrates. *In*: Genetics, Paleontology, and Evolution, Ed. by G. L. Jepsen, G. G. Simpson, and E. Mayr. Princeton Univ. Press, Princeton, New Jersey.

GOLDSCHMIDT, RICHARD 1927 Physiologische Theorie der Vererbung. Springer, Berlin.

A COMPARATIVE FUNCTIONAL ANALYSIS OF PRIMATE SKULLS BY THE SPLIT-LINE TECHNIQUE *

BY N. C. TAPPEN

Graduate School of Medicine
and
Evans Institute of Dentistry of the University of Pennsylvania [1]

THE mammalian skull serves to house and protect the brain and the organs for the special senses of sight, hearing, taste and smell; to provide inlets for food, water and air, plus passageways for blood vessels and nerves; to provide for biting and chewing food, and at the same time to give attachments for the chewing muscles and a bony framework to resist the forces that are set up by the masticatory apparatus; and to give attachment for the muscles which move the head and maintain its carriage. In order to survive the animal must be able to have all these functions operating in harmony. It is probable that compromises between them are in places necessary. It is certain that they can affect each other in some degree.

The skull must therefore be thought of in terms of its relationship to many bodily functions, realizing that it is affected by many factors. This complexity is partly counterbalanced by its remarkable geographic character, by which the location, interrelationships and operations of many vital organs can be deduced. As examples, the roof of the mouth is the floor of the nose, and the origins and insertions of chewing and head-moving muscles frequently leave their marks on the bone, allowing an evaluation of their strength and the direction of their contraction. The value of the skull for analysis of vital processes is most vividly illustrated in the paleontological record, where it is possible to make

* This project was supported by a grant from the Wenner-Gren Foundation.

[1] Present address: Department of Anatomy, Emory University.

meaningful comparisons between the skulls of animals which we have never seen alive. However, progress in the interpretation of the evolution of the skull must depend in large part on the methods of analysis available on living forms, and the development of new techniques is vital to the advancement of biological science as a whole.

The bone in the skull has other levels of organization not observable in the gross structures, offering methods of analysis which carry beyond those of ordinary observation. One promising aid to functional analysis is the split-line technique. It demonstrates the organization of the compact surface bone by staining methods. Benninghoff ('25) was able to show in a human skull that some areas of the bone, such as in parts of the face, were organized in their split-line patterns while other areas, such as the skull-cap, were not.

The technique is described extensively elsewhere (Seipel, '48; Tappen, '53). The bone is decalcified in dilute acid until it is soft and rubbery enough to allow easy penetration by a needle. Usually splits result rather than round holes, because bone has a minute "grain" analogous to that of wood. India ink is then put into the fissures to clarify their direction. Benninghoff ('25) and Seipel ('48) showed histologically that the splits correspond to the direction of organization of the majority of the Haversian systems in the region punctured. Haversian systems are the basic means of supplying blood to compact bone. They consist of very minute central blood vessels with concentric layers of bone called "lamellae" surrounding them.

Benninghoff and other workers used intermittent punctures in producing their split-lines. This gave an incomplete picture, since branchings, divergencies and the meeting points of different split-line systems could not be accurately traced. There is reason to believe that they were at times led into errors of interpretation because of the inadequacy of their technique. Seipel ('48) made a great improvement by joining his split-lines with further intermediate punctures in those regions in which patterns were distinct enough to warrant it. This method was followed in the present study.

In well-organized regions it was found that a further refinement was possible. The point of the needle was pushed into the bone two millimeters or less, then pulled in the direction of the original split. In this way long split-lines could be made quickly, and the actual deviations of the Haversian system organization could be traced more accurately. It was also found that directional organization in regions

of very thin bone could be ascertained in this manner, where punctures with needles of even very thin diameter frequently gave no pattern, presumably because of the crushing effect. It was thus possible to obtain patterns in such regions as the tooth sockets in small specimens.

It is necessary to use this innovation with caution. Frequent tests were necessary to make certain that the needle would go only in one direction. In only one region of one specimen was it found possible to pull the needle in almost any direction.

In an earlier work (Tappen, '53) it was found that decalcification affected the teeth more than other parts of the skull, destroying the enamel very quickly. In order to preserve the appearance and continue study on the occlusal relationships of the specimens, dental beewax was melted and used to cover the teeth, sealing them off from the acid. This method is also recommended to workers interested in keeping parts of skulls intact while decalcifying other parts.

The biological meaning of the Haversian system organization revealed by the split-lines is far from being completely understood. Theoretical discussions may be found in Benninghoff ('27), Murray ('36) and Seipel ('48). Work along these lines has been sporadic, mainly descriptive, and has been accompanied by little experimental work to determine causes. The general assumption has been that they are somehow related to mechanical forces, pressure and tension, which are acting upon the bone. As will be seen, this assumption makes a good deal of sense in some areas of primate skulls, but other areas are not readily explained on this basis and other factors seem to influence the direction of the lines.

Some of the most indicative investigations are those in which split-line preparations were made on bone which suffered functional alteration during life. Benninghoff ('27) found changed patterns in a femur bent by rickets, and Seipel ('48) found that the patterns in a mandible, broken and imperfectly reset, adapt their direction to the change. It thus appears that split-line patterns can actively change during the life of the individual. Definitive controlled experiments have not been made, however.

In order to proceed from the relatively familiar to the unfamiliar, and to maintain the basic orientation of this non-human primate symposium on problems relating to man, the split-line pattern in the human face may be briefly described. Figure 1 is from Tappen ('53). The pattern of lines immediately above the tooth row parallels the alveolar

margin. Immediately above, all the lines in the face ascend, the ones from the molar region paralleling the zygomatico-alveolar crest and the others tending to parallel the nasal opening. These divergent systems are interrupted by a continuous system of lines beginning at the frontal process of the maxilla, coursing along the infraorbital region and continuing through the zygoma to the region of origin of the anterior tendinous portion of the masseter muscle. This has been interpreted as meaning that the pull from the muscle is of primary importance in counteracting the stresses from the pressure of the tooth row, and that the infraorbital, zygomatic and lateral orbital regions are primarily

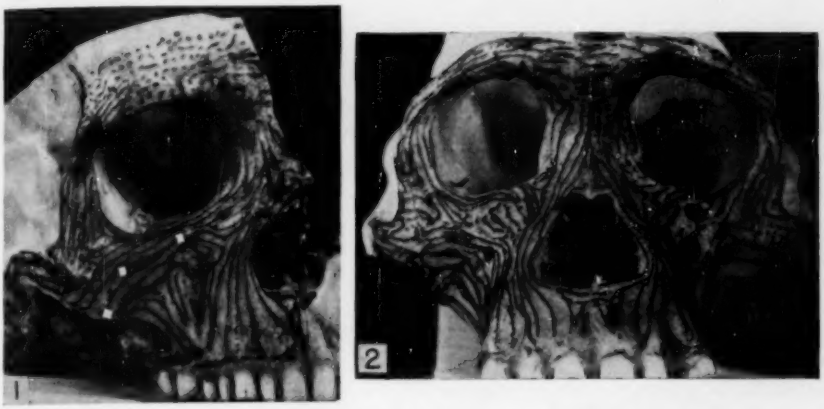


FIG. 1. SPLIT-LINE PREPARATION ON HUMAN FACIAL SKELETON.

FIG. 2. SPLIT-LINE PREPARATION ON CHIMPANZEE FACIAL SKELETON.

under tension from the downward pull of the exterior chewing muscles. This is in direct opposition to the generally expressed view (Hooton, '46) that the lateral orbital and brow ridge area resist upward chewing pressures. It may also be noted that the human brow ridge shows little or no organization. From this kind of information it was postulated that structures such as the infraorbital bar represent functional responses to stress while such structures as the brow ridges probably do not.

The chimpanzee patterns, shown in figure 2, differed strongly enough from those in man to suggest correlations with differences in gross structure and with relationships between different parts. Specifically, there are no completely divergent systems of split-lines in the lower face. Instead of an infraorbital-zygomatic system of lines cutting off the ascending patterns, the ascending lines continually branch off laterally

toward the region of origin of the masseter muscle, the deviation being at a progressively higher level the farther the lines are away from the muscle. Finally, some lines enter the orbit, and others continue up the interorbital region to the brow ridge. These differences may be related to the longer face, absence of elevated nasal bridge, and lower origin of the masseter muscle in relation to the orbits. It is also possible that this clarifies the occasional appearance of the canine fossa in man and its absence in the chimpanzee, since there is implied a relatively unstressed area between three divergent split-line systems in man but not in the chimpanzee. It will also be noted that the split-lines in the chimpanzee brow ridge are strongly marked and continuous with the lines in the lateral orbital region. This has been taken to indicate that the brow area in the chimpanzee is an important stress-bearing structure, and that it resists tension from the downward pull of the temporal and masseter muscles. It is also indicated that this is so because there is no forehead region above the orbits to absorb and distribute these stresses, as is the case in man. In actuality, the chimpanzee face and braincase grow apart during development of the animal. Seipel ('48) has shown that the split-line pattern is already developing in the brow region of a three-year-old chimpanzee, however.

So much data of relevance to the understanding of the primate face resulted from comparative split-line analysis of one ape that work with other non-human primates seemed imperative. Only the chimpanzee has been described in more than the barest features. Accordingly, split-line preparations were made on widely differing representatives of the order. I am indebted to the Wistar Institute of Anatomy and Biology for lending single specimens of *Simia satyrus* (probably male), *Hylobates mulleri* (female), *Macacus cynomolgus* (male), *Semnopithecus femoralis* (sex unknown), *Ateles* (male, species unknown) and *Lemur mongos* (sex unknown). All these animals had full permanent dentition in good occlusion. Mr. Harold Green of the Academy of Natural Sciences, Philadelphia, donated the specimen of a young gorilla, sex unknown. Only the first molars are erupted in the permanent dentition. The preparations include the mandible, braincase and skull base as well as the mid-facial region, although these were done on both sides only when the pattern proved to be very interesting.

Detailed description and analysis of this material must await a later publication. Some of the salient features of these specimens can be reported here within the limits imposed by the time allotted and the

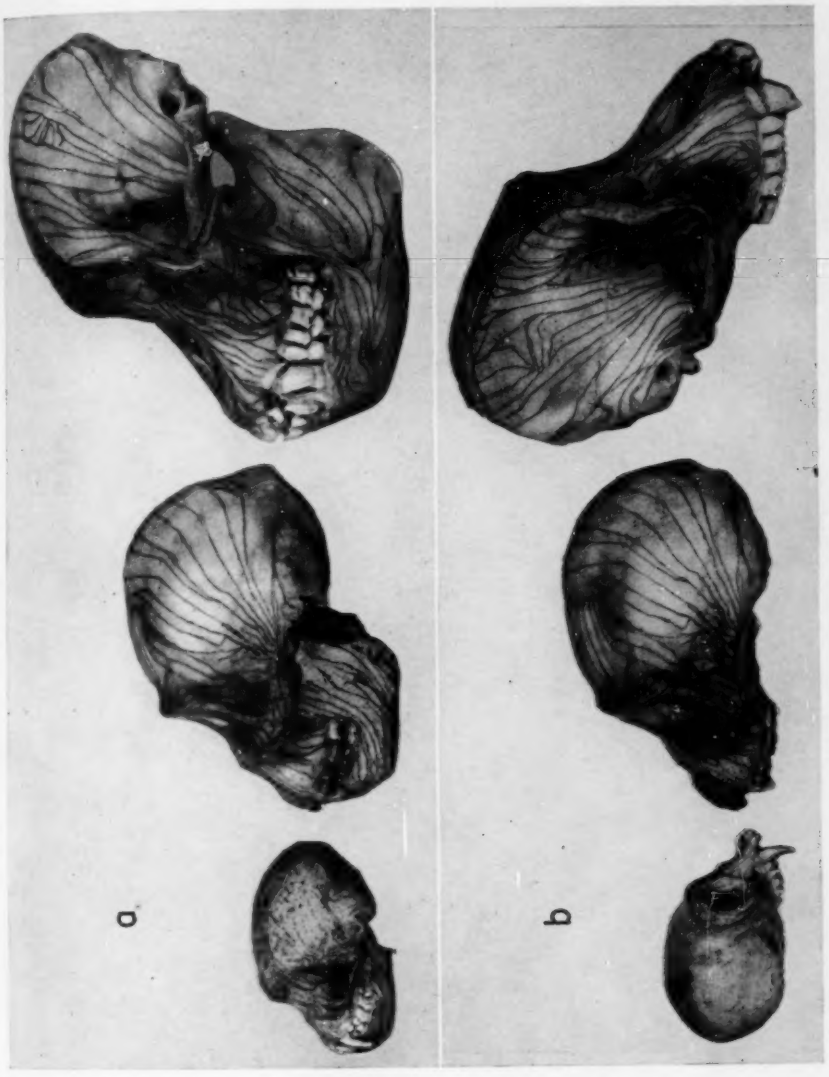


FIG. 3A and B. LATERAL VIEW OF SPLIT-LINE PREPARATIONS ON THE SKULLS OF ADULT GIBBON, JUVENILE GORILLA AND ADULT ORANG UTAN.

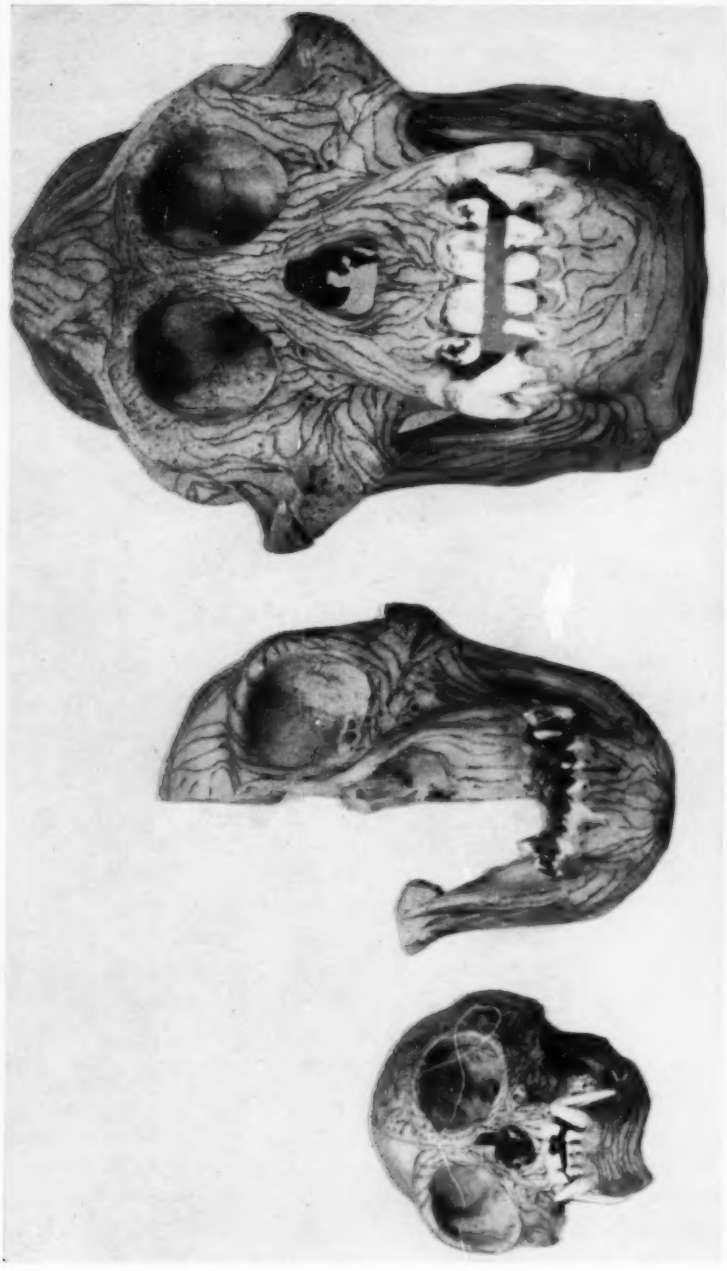


FIG. 4. ANTERIOR VIEW OF SPLIT-LINE PREPARATIONS ON THE SKULLS OF ADULT GIBBON, JUVENILE GORILLA AND ADULT ORANG UTAN.

Juvenile Gorilla and Adult Orang Utan.

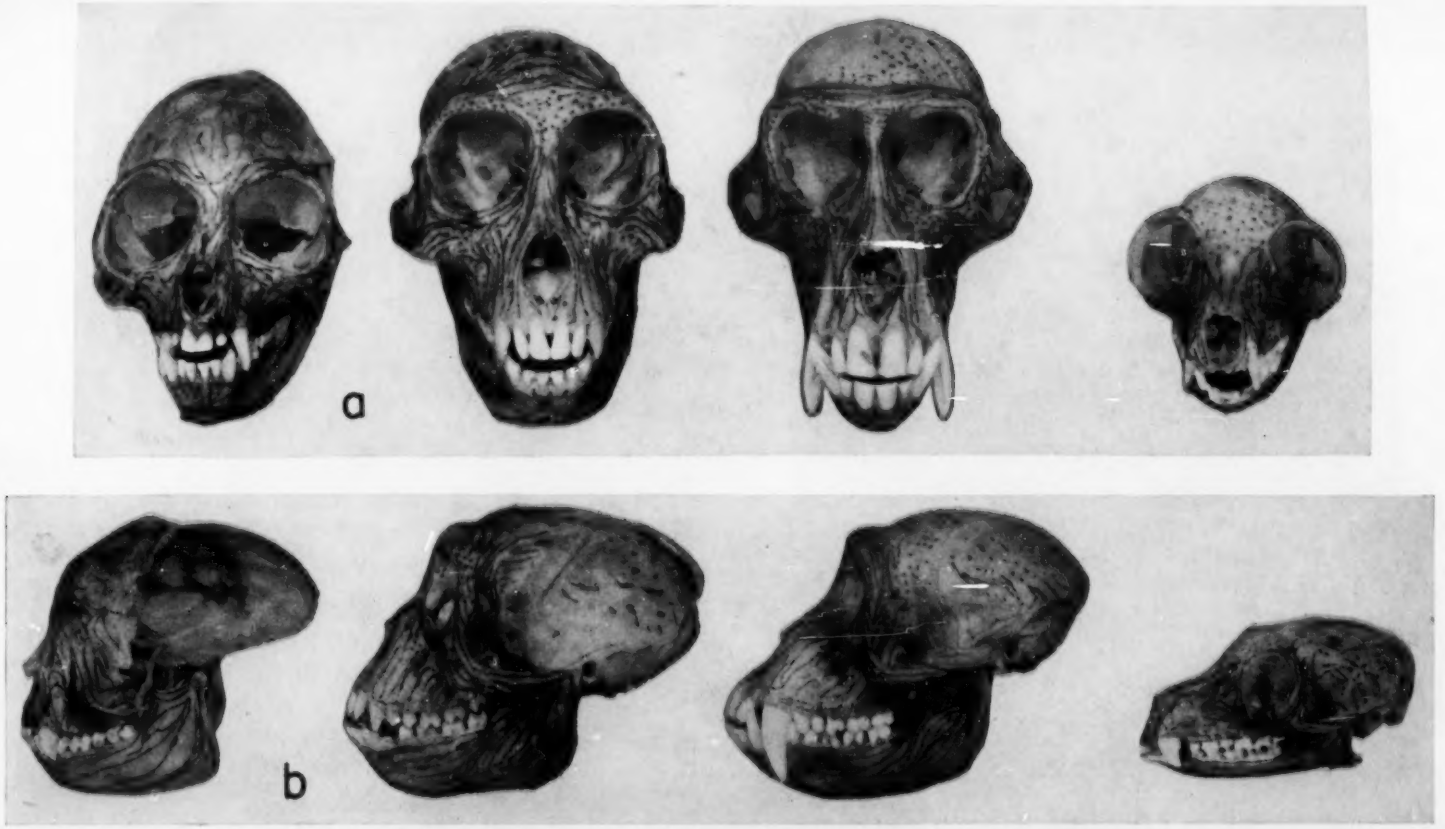
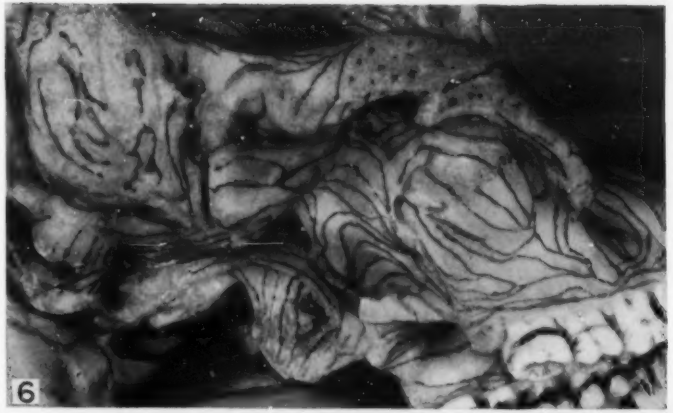


Fig. 5. Split-Line Preparations on the Skulls of Spider Monkey, Langur, Macaque and Lemur.
A. Anterior View. B. Lateral View.



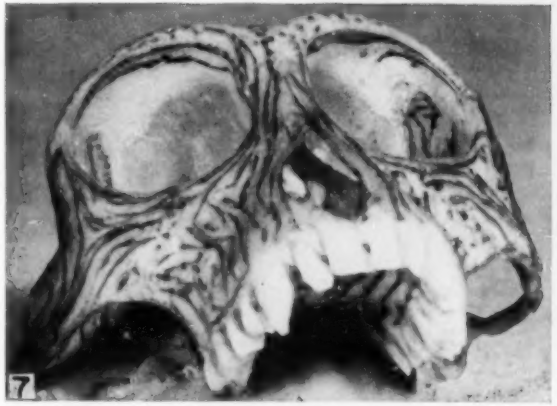


FIG. 6. SPLIT-LINE PREPARATION IN THE BASAL REGIONS OF THE ORANG UTAN CRANIUM.

FIG. 7. SPLIT-LINE PREPARATION ON CRANIUM OF LANGUR, SHOWING ORGANIZED PATTERNS INSIDE THE BORDERS OF THE ORBIT.

FIG. 8. SPLIT-LINE PREPARATION ON MANDIBLE OF SPIDER MONKEY, SHOWING LINES ON BOTH SIDES OF RIGHT RAMUS AND CORPUS. PATTERNS ARE AT RIGHT ANGLES TO EACH OTHER IN THE REGION OF INSERTION OF THE INTERNAL PTERYGOID MUSCLE.

THE ORBIT.

FIG. 8. SPLIT-LINE PREPARATION ON MANDIBLE OF SPIDER MONKEY, SHOWING LINES ON BOTH SIDES OF RIGHT RAMUS AND CORPUS. PATTERNS ARE AT RIGHT ANGLES TO EACH OTHER IN THE REGION OF INSERTION OF THE INTERNAL PTERYGOID MUSCLE.

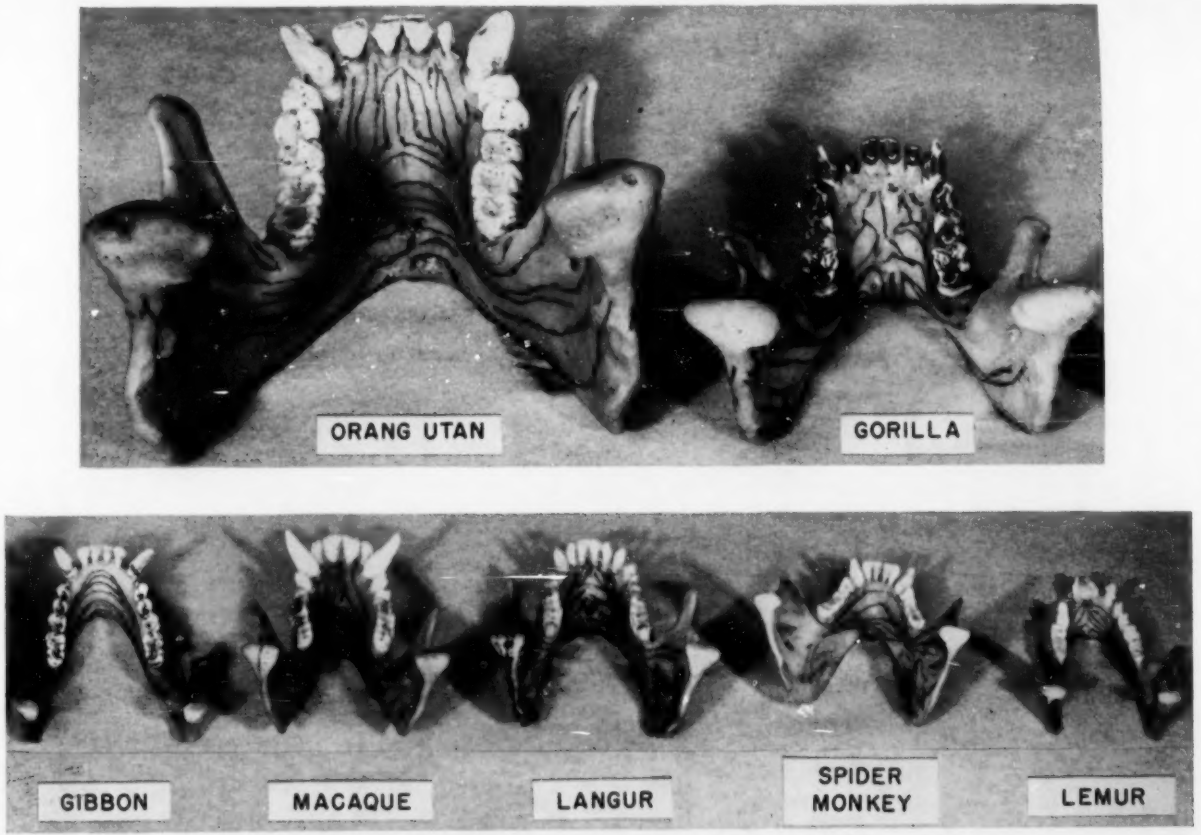


FIG. 9. SPLIT-LINE PREPARATIONS ON MANDIBLES.

review nature of this article, however. A number of split-line characteristics are relevant to problems raised by the comparisons made between man and the chimpanzee, and other problems are revealed.

Viewed from the side, (figure 3A) the gibbon shows locally organized patterns in the area bounded by the temporal muscle but no overall regularity. This is in a number of respects similar to the human situation reported by Benninghoff ('25), although he found definite patterns associated with the human temporal lines. The orang utan and the gorilla, on the other hand, show continuous lines which appear to correspond generally to the fan-like spread in the direction of the fibers of the temporal muscle. These end at the temporal lines in the orang utan, but merely deviate at this level in the gorilla, continuing to the sagittal suture.

The relationship of this pattern to the pull of the temporal muscle is strikingly evident, but two bilateral deviations from the general picture in the orang utan indicate that factors other than mechanical forces can be acting to organize the bone. (Figure 3B). Well up on the parietal bone a sudden change gives a local area of radiation which may correspond to the direction of growth of the bone from its original ossification center. Ahrens ('36) found that split-line patterns in the human fetal and infantile cranial vault correspond to the direction of growth of the original bone, radiating from the original ossification centers. By the age of seven years, however, the lack of organization in the adult observed by Benninghoff ('25) was already apparent. The other deviation from the general pattern corresponding to the temporal muscle may be observed in the frontal bone as it meets the lower part of the parietal. Here the split-lines turn toward the suture. Above this the suture has become united, and the lines ascend in conformity to the general pattern. It is therefore indicated that lines turning toward the suture are somehow related to that suture, either because of the direction of bone growth, local stresses at the suture, or some other cause.

It is possible that preparation of the inside of the skull vault might reveal relevant information on these problems of deviation from simple muscle-response pattern, but this could not be done on these specimens.

The lines in the gorilla brow ridge deviate more and more toward the side as the region adjacent to the temporal muscle is approached. It is suggested that the area is coming more and more under the influence of the encroaching temporal muscle during the growth of the individual. Eventually the temporal muscle reaches the midline in many gorillas.

It seems possible that the brow ridge area is in transition in its split-line patterns, and that in the adult animal the split-lines would have been continuously horizontal across the brow ridges, as in the chimpanzee. The adult skulls in the two species are very similar in form. The possible rearrangement suggested emphasizes one of the many potentialities of the use of split-line analysis of growth patterns in primates. This is a line of investigation that has only begun to be utilized.

The exterior of the zygomatic arch in the orang utan shows very few organized split-lines on either side. In all other animals processed this area has yielded highly organized splits, yet the lack of splits was predicted before decalcification. The bone here was rough and slightly pitted, resembling unorganized bone frequently found at the human brow ridge and mental protuberance. On the internal face of the arch, however, the split-lines are well defined, paralleling the axis of the arch. The organization of the deeper layers cannot be determined on this specimen, since it is on loan and must be returned.

The close-up picture of the pterygoid and maxillary tuber regions of the orang utan (figure 6) is very revealing as to the relationships between the split-lines, chewing pressures and the pull of the chewing muscles. The lines progressing backward in the maxillary tuber cross over toward the pterygoid process of the sphenoid bone above the third molar. The bone encasing the maxillary sinus here is thicker than it is both above and below. Lines are continuous with these in the pterygoid process of the sphenoid bone, indicating a functional reality for the pterygoid pillar (Weinmann and Sicher, '47). This probably represents a response to the compressive force from the molar teeth. Immediately behind, however, these lines loop back and down in the lateral pterygoid plate, almost certainly in response to the downward pull of the internal pterygoid muscle which originates along its internal face. Those lines which continue upward above this are then turned posteriorly and laterally in the infratemporal fossa, probably under the influence of the external pterygoid muscle originating in this area. Just anterior to this, lines which have ascended in the infratemporal surface of the maxilla deviate backward to end at the infratemporal crest. These also are probably responding to the pull of this muscle. These lines are at right angles to the lines associated with the temporal muscle immediately above. If these interpretations are correct, a number of different forces are analyzed into the areas they predominantly influence.

The pattern at the central portion of the mandible (figure 4)

resembles that reported for man by Seipel ('48) most closely in the orang utan. The split-lines at the base continue from one side to the other, while those closer to the lower incisor teeth generally ascend. In the gorilla the lines coming in from the body of the mandible converge on each side and do not cross the midline. Ascending lines begin at the very base of the symphyseal region. In the gibbon the lines which cross over predominate.

In human beings with well-developed mental protuberances Seipel ('48) found that the bone yielded no definite split-line patterns. He explained this as being the result of the meeting of trajectorial systems at this region. When the surface bone was dissected away, however, he found the regular pattern of lines going across the midline at deeper levels.

None of the specimens processed here shows such a pattern. Other regions of the skull show definite areas where different split-line systems meet without disorganization of the bone. Unorganized bone can be next to bone with well-developed split-lines where a simple stress pattern is indicated. It therefore seems probable that the piling on of unorganized bone has some other explanation than one related to responses to mechanical stress.

It is interesting to note that Henckel ('31) made split-line preparations on the lower jaw of a gibbon, an orang utan and a different species of *Semnopithecus*. He found that the external symphysis region in these forms had split-lines running vertically rather than from one side to the other. He related this difference from man to the difference of the angles at which the mandibular halves come together at the midline. It will be noted that all three of these forms in the present series have basically the same pattern as man. Henckel apparently found a pattern which is highly variable rather than diagnostic.

In the orang utan and gorilla the lines from the incisor and canine teeth ascend into the nasal cavity or parallel its lateral borders to ascend to the brow region between the orbits. In the orang utan they die out just above the fronto-nasal suture, but in the gorilla they continue back on the frontal bone after being deviated somewhat to the right at the top of the developing brow ridge. The divided orang utan brow ridges have no decided split-line patterns, and usually the punctures do not form splits at all. Immediately posterior is a narrow transverse split-line pattern, which is succeeded by lines coursing backward between the superior temporal lines. These continue back to the nuchal area, where

lines continue downward toward the foramen magnum. This region is invaded by the lines along the side of the braincase only as the nuchal area is approached. In the gorilla the lines continue back only as far as the frontal bone extends. Laterally they seem to be deviated by the pull of the temporal muscle, while the split-lines are quite irregular toward the midline. Behind the frontal bone the lines associated with the pull of the temporal muscle continue across to the midline.

Some interpretation of these patterns can be given, but so much remains a problem that the crudity of split-line studies in their present state is emphasized. The patternless state of the small orang utan brow ridges indicates that their formation has little to do with facial stresses, as in man. Here there is a distinct forehead in the same general plane as the face. The meaning of the split-lines coursing backward is not clear to the writer. Is it from chewing pressures, from the pull of nuchal musculature, or a pattern not related to mechanical stresses? The lines just behind the brow ridges extending laterally would indicate tension in that direction, and favor a tensile explanation. However, the backward direction of the lines in the gorilla frontal bone probably represents a continuation of pressures. Certainly there is no continuation to the nuchal area. The great need for developing instrumental tests of the strains taking place in the bone of living animals during normal functioning is particularly revealed by these dubious areas. Electric strain gages have been used by Evans ('53) for this purpose in the tibia of a dog, but the usefulness of the instrument in biology is yet to be fully realized.

The orang utan resembles the chimpanzee in the infraorbital and zygomatic regions, while the gorilla and gibbon have the laterally-directed patterns found in man. Ascending split-lines in the face of the gibbon do not appear to reach the interorbital region. The lines in the posterior part of the maxilla parallel the alveolar border.

Comments on the remaining primates must be confined to a few general considerations. On the brow ridges, the macaque appears to resemble the chimpanzee closely (figure 5A), with a large continuous brow ridge set somewhat apart from the braincase and the split-lines running continuously in it. In the langur (*Semnopithecus*), however, the supraorbitals are small, divided, and lacking any pattern of lines. Instead, the stress from the chewing muscles must be taken up behind in the frontal bone, if the continuous coronal split-line pattern is any indication. The macaque, on the other hand, has no organized patterns

behind the brow ridge. It is thus apparent that the supraorbital region is very different in some aspects of its functioning in the two forms, as is also the case in the chimpanzee-human comparisons. These different patterns of organization indicate that experimental work on different primates can give answers to many of the problems of the relationship of the supraorbital area to other regions and of the functions of that area in general.

The lemur also has no split-lines in the interorbital region in the frontal bone, except very close to the orbits. The spider monkey has light, divided brow ridges and a considerable forehead, but the supraorbital region has organized split-lines.

The lateral view of these specimens (figure 5B) shows rather vividly the continuation of lines of the lemur zygomatic arch forward on the maxilla. Anterior to this, the pattern dies out. These lines are here regarded as being a response to the pull of the masseter muscle which seems to have a strong antero-posterior direction in its anterior fibers This may be another, more extreme example of tension systems of split-lines from the muscle overcoming upward pressures. Actually no ascending split-lines are apparent in this region. It may be observed that the gibbon has a somewhat similar system of lines in the maxilla, and that the low ramus of the mandible gives an antero-posterior direction to the masseter muscle. Here once again ascending lines are not apparent behind the canine teeth.

The lines in the *Semnopithecus* frontal bone previously mentioned are directed toward the lateral orbital region. Externally, this area has no organized split-lines above the zygomatic bone, the pattern being resumed below the suture. However, figure 7 shows that the pattern continues on the orbital side of the frontal bone in this area. This suggests that the stresses in the region are continuations of the general tension system associated with muscle pull, which are reflected in the bone organization at deeper levels here, but that unorganized bone is piled on laterally as in the zygomatic arch of the orang utan.

The close-range photograph of the spider monkey lower jaw (figure 8) is interesting because its transparency allows one to see how the split-lines on opposite sides of single structures conform to each other in some places and deviate in others. The fainter lines paralleling the mandibular notch are on the lateral side, while the ascending darker lines which cross them are on the side facing the viewer. Farther back on the ramus the lateral and medial lines coincide closely. However, the

deviant pattern between the angle of the jaw and the last molar is apparent. The lines descending toward the inferior border of the mandible in two groups are accompanied by a definite thickening of the bone. These are presumably associated with the insertion of the internal pterygoid muscle. The lines on the lateral surface can be seen through the bone even here. This figure illustrates vividly the precise differential response to closely juxtaposed organizing factors revealed by the split-lines.

The mandible is primarily a stress-bearing organ, and it usually has the most completely organized split-lines in the face. The view (figure 9) of the inside of the symphyseal regions shows that nearly all the specimens have lines running across the midline in the basal region. In those specimens in which there is some degree of anterior protrusion, the lines run forward and upward. This is most noticeable in the lemur, orang utan and macaque. The latter two show nearly all their tooth wear on the incisors, and the bone in this region is very massive in both specimens. It is difficult to avoid the inference that the greatest chewing stresses are up in this region in the two specimens.

Split-line patterns have been found in all mammals investigated to date. Common laboratory animals can thus be used in basic experiments on the nature of the Haversian system organization in bone. One has been attempted by the writer, and others are planned. The differences in external appearances and split-line organization of the surface bone in different areas noted in this study indicate that basic histological studies could yield important information. New techniques to supplement split-line analysis are needed, since this is after all a relatively crude approach. Improvements in the technique itself are a crying need. It is at present very tedious and time-consuming. This small project alone involved several hundred man-hours to prepare. The development of a device to make the splits and administer the color at the same time would help enormously. Injection and corrosion preparations are possible for studies of local areas with the use of new techniques being developed by Dr. Batson of Pennsylvania, and new methods of vital staining are now available to help studies of bone growth.

Variations in split-line patterns in man are gradually being revealed as more specimens are processed. This study gives no idea of the variability of patterns and their relationship to form variation within the species processed. Museums are understandably reluctant to give out specimens which will not be returned intact. Even in this study, the

organization of deeper layers of bone must remain a matter of speculation. The necessity for modern primatologists to obtain their own collections is abundantly clear, since only in this way can they get adequate samples from populations and process them as they see fit.

The relationship between the patterns in the bone and soft tissues such as muscles, ligaments and connective tissue can only be guessed at in these specimens. This points up another great need for primate work, the study of soft parts on the same individual in which the skeleton is studied. When hypotheses as to the soft-tissue situation are set up on the basis of split-line analysis of the bone, they can then be tested on other specimens. Only in this way will the functioning organism be understood as anything more than a jumble of unrelated parts.

The variations in form and split-line patterns between the primates processed in this study are quite striking, as the figures reveal. It is also possible to offer plausible functional explanations of some of them. With the further development and application of the method, it should be possible to apply it to problems of the form of fossil primates and hominids. The wide variations to be found within the order offer functional situations very similar to variations in living races and those indicated in fossil man. For example, in this sample there are projecting malar regions similar to Mongoloids (Hooton, '46), and backward-shelving ones similar to Neanderthal man (Howell, '51). When enough such situations have been analyzed, it may be possible to generalize about the relationships of the region to other parts of the skull and to the functional muscle-bone systems implied by them. If a partial genetic analysis is made possible by the technique, taxonomic connections may be traceable with greater certainty, and the processes involved during human evolution should be understood with much greater clarity.

The establishment of functional systems offers possibilities for the genetic analysis of form in primates and man. Where the relationships between different parts of the skull suggested by the split-line patterns are tested by experimental work, the number of genes implied in the determination of form is greatly reduced. This is because the interrelationship implies a single process operating to influence the various parts affected.

Functional analysis with split-lines may be a further aid in the genetics of form. Those structures which have no definite patterns can in all likelihood be said to be unmodified by mechanical stresses, one of

the environmental factors complicating genetic analysis. Others which have a split-line structure, such as the infraorbital bar, can probably be evaluated by experiments as to the extent to which they are a response to stresses or are independently genetically determined.

The previous discussion has indicated how the split-line technique may help to disentagle the primary genetic and the secondary functional causes of form in various regions of the skull by comparisons of different primates, and how this may apply to the interpretation of the variations to be found in man, both living and fossil. The potential uses of non-human primates for these purposes have scarcely been realized, however, going far beyond the limitations of the technique described here. At the very foundation of this potential is the previously unrealized possibility of expanding the scope of human genetics tremendously through the experimental breeding of non-human primates. It seems highly probable that a great many human genes can be elucidated through their homologues in other primates. And since there are many living primates which are pre-adapted for the dramatic steps assumed in human evolution, it may also be possible to reproduce many of these steps through creation and selection of mutations and selection of favorable gene combinations in breeding experiments. It may thus be possible to isolate the actual genetic changes involved in the development of such features as stereoscopic vision, development of brachiating habits, assumption of upright posture, loss of inherited behavioral traits, speech, and the general potentialities for symbolic learning and cultural behavior. This would be important in developing a truly genetic primate taxonomy and in interpreting the fossil and archeological record. More important, however, would be the revelations of the functioning genetic systems in human beings, reflected back by discovery of the processes that were probably involved in their development. At a somewhat less pretentious level, it should be possible to use primate genetics in combination with split-line experiments in further clarifying the relationship between the form and functioning of the minute architecture and gross morphology of the human skeleton.

LITERATURE CITED

AHRENS, H. J. 1936 Die Entwicklung der Spaltlinienarchitektur des knöchernen menschlichen Schädels. Morphol. Jahrb., 77: 357-371.

BENNINGHOFF, A. 1925 Spaltlinien am Knocken, eine Methode zur Ermittlung der Architektur platter Knochen. Anat. Anz. (Ergänz. heft), *60*: 189-206.

——— 1927 Über die Anpassung der Knochenkompakta an geänderte Beanspruchung. Anat. Anz., *63*: 289-299.

EVANS, F. G. 1953 Methods of studying the biomechanical significance of bone form. Am. J. Phys. Anthropol., n. s. *11*: 413-435.

HENCKEL, K. O. 1931 Vergleichend-anatomische Untersuchungen über die Struktur der Knochenkompakta nach der Spaltlinien-methode. Morphol. Jahrb., *66*: 22-45.

HOOTON, E. A. 1946 Up From the Ape. 2nd edition. Macmillan, New York.

HOWELL, F. C. 1951 The place of Neanderthal man in human evolution. Am. J. Phys. Anthropol., n. s. *9*: 379-416.

MURRAY, P. D. F. 1936 Bones; a study of the development and structure of the vertebrate skeleton. Cambridge University Press, Cambridge.

SEIPEL, O. M. 1948 Trajectories of the jaws. Acta Odontologica Scandinavica, *8*: 81–191.

TAPPEN, N. C. 1953 A functional analysis of the facial skeleton with split-line technique. Am. J. Phys. Anthropol., n. s. *11*: 503-532.

WEINMANN, J. P. AND H. SICHER 1947 Bone and Bones. C. V. Mosby, St. Louis.

METRIC AND MORPHOLOGIC VARIATIONS IN THE DENTITION OF THE LIBERIAN CHIMPANZEE; COMPARISONS WITH ANTHROPOID AND HUMAN DENTITIONS

BY E. L. SCHUMAN AND C. L. BRACE

The Department of Oral Pathology
The School of Dental Medicine and Peabody Museum
Harvard University

THE largest known collection of chimpanzee crania and calvaria (291 in all) from a single area, northeastern Liberia, provides an unusual opportunity to study in detail the dentition of the chimpanzee. Dr. George W. Harley of Ganda, Liberia, secured the collection for the Peabody Museum, Harvard University, and in turn it was made available to us by Dr. Earnest A. Hooton for our studies on the dentition. Investigations have been conducted of both the macrostructure (metric and morphologic details) and the microstructure of chimpanzee teeth. The latter has been described in a preliminary report (Schuman and Sognnaes, '52). This paper is an assessment and evaluation of the metric and morphologic variations of chimpanzee dentition.

Part I (Metric) consists of a recording of dimensions: their means, ranges, standard deviations, coefficients of variation, modules, indices (talonid-trigonid, length-breadth). These data are compared to similar data of anthropoid and human dentitions.

Part II (Morphology) lists observations on mandibular molar patterns and the hypocone and cingulum of maxillary molars. Comparisons are made to similar observations from human groups.

PART I

METHODS

Mesial-Distal Diameter: (Length) In molars this measurement is taken between the mesial and distal contact points and on an axis mid-way between the buccal and lingual surfaces. In incisors, this measurement is taken as the maximum between mesial and distal contact points and is referred to as "width."

Buccal-Lingual Diameter: (Breadth) It is the maximum buccal-lingual diameter on an axis perpendicular to the plane used for the mesial-distal measurement.

Cervical-Incisal Diameter: (Height) This measurement is taken on the labial surface as nearly parallel to the vertical median crown axis as possible from incisal tip to lowest cervical point of enamel.

Talonid-Trigonid Diameters: These are breadth diameters in the mandibular molars of the posterior and anterior moieties respectively. Each is measured at the maximum breadth irrespective of the perpendicular to the length plane. The trigone is slightly wider than the usual maximum breadth (described above) except in mandibular M_1 where the talone is the broader measurement.

Mesial-distal and buccal-lingual measurements of the maxillary and mandibular molars, the maxillary premolars, and the mandibular second premolars were taken. Measurement of the mandibular first premolar were omitted, since this tooth is so skewed and variable in form as to make repeated accurate measurements unfeasible. Also, the mandibular first premolars in human dentitions are not comparable to those of the anthropoid apes.

The mesial-distal diameter in the case of the canine is unlike that taken of the molars and premolars. In chimpanzee canines, the maximum mesial and distal points are found close to the cervix of the crown; in human canines, this maximum diameter is nearer the incisal tip.

Incisors have been measured only in the mesial-distal diameter. Cervical-incisal diameters were not available in sufficiently large samples due to the fact that usually all incisors had undergone attrition to a point where accurate measurement of the height of the crown was not feasible.

In general, the methods of measurement described are similar to those utilized by investigators whose data are compared with ours. All measurements were taken with the Boley gauge, which is a small sliding caliper, calibrated to 0.1 mm and used chiefly by orthodontists. For our purpose, the gauge was modified by grinding the beaks fine, so as to produce measurements of greater accuracy.

Repeated measurements on the same teeth at various times produced an average error of 0.2 mm. This compares favorably with that of Pedersen ('49) who states that on repeated measurements by the same person, the difference was at most not more than 0.2 mm. Nelson ('38), on the other hand, maintains that a metrical accuracy of 0.1 is easily attained in mesio-distal and labial-lingual dimensions but that an accuracy of greater than 0.3 mm cannot be obtained for crown height. However, Nelson does not make clear whether this degree of error

was arrived at after testing repeated measurements on the same teeth. Less optimistic is Shaw ('31) who says that it is impossible to obtain accuracy better than 0.5 mm.

Measurements were made only on teeth in which the degree of attrition had not altered the original dimensions.

In general, teeth on the right side were selected for measurement. Where intact groups of teeth were not available on the right side, teeth from the left side were measured. This did not affect the results, since in testing it was found that there was no significant difference between right and left measurements. Ashton and Zuckerman ('50) also found no sigfinicant difference between right and left teeth.

METRIC DATA OF LIBERIAN CHIMPANZEE DENTITION

Table 1 contains the metric data of the maxillary and mandibular molars and premolars (mandibular first premolar excluded) of the Liberian chimpanzee. The symbols M_1, M_2, M_3 refer to first, second and third molars respectively. PM_1 and PM_2 refer to first premolar and second premolar. The values for female and male specimens are listed separately, as are their combined values. All female mean dimensions are smaller than male. These mean differences were tested for significance according to Snedecor's formula ('50, p. 81). The breadth diameters of male maxillary molars, maxillary premolars, and mandibular M_3 are significantly greater than those of the female. In mandibular M_1, M_2, PM_2 the breadth diameters of the male approach borderline significance over those of the female. It would seem therefore that all the male molars and premolars tend to be significantly broader than those of the female. Significance in length diameters favoring the male were found only in three of 9 teeth: maxillary M_2, M_3, mandibular M_1, none of the premolars exhibiting this significance. None of the female length diameters were significantly greater than those of the male. Ashton and Zuckerman ('50, p. 472) in their measurements of orang-utan, gorilla and chimpanzee dentitions found that " in all the dimensions which are not affected by attrition, every male tooth is larger than the corresponding female tooth."

In table 1, the mesial-distal (length) diameters diminish proceeding from maxillary M_1 to M_3, and from maxillary PM_1 to PM_2. If the means of the buccal-lingual (breadth) diameters are corrected to one place [1] (as they are for comparisons to other groups), M_1 and M_2 do

[1] Two decimal places have been maintained for the record, but are of little practical value, since the measurements themselves were taken to 0.1 mm and the average measurement error is 0.1 mm.

TABLE 1

Dimensions and Variations in Liberian Chimpanzee Dentition

		MAXILLARY TEETH										
		Mesial-Distal					*Buccal-Lingual*					
		N	Range	Mean	S. D.	C. V.	N	Range	Mean	S. D.	C. V.	Module
M_1	Total	226	9.0-12.6	10.70	0.54	5.0	225	9.9-12.7	11.57	0.48	4.1	11.13
	♂	132	9.0-12.3	10.73	0.58	5.4	132	10.6-12.7	11.66	0.48	4.1	11.19
	♀	94	9.5-11.8	10.66	0.47	4.4	93	9.9-12.6	11.46	0.48	4.2	11.06
M_2	Total	229	8.7-11.9	10.25	0.59	5.8	228	10.0-13.6	11.62	0.59	5.1	10.93
	♂	132	9.0-11.9	10.37	0.60	5.8	131	10.5-13.6	11.76	0.64	5.4	11.06
	♀	97	8.7-11.9	10.12	0.58	5.8	97	10.0-12.6	11.44	0.57	5.0	10.78
M_3	Total	208	7.3-11.8	9.34	0.69	7.4	209	9.2-13.2	10.86	0.64	5.9	10.11
	♂	120	7.3-11.8	9.55	0.69	7.2	121	9.3-13.2	10.90	0.64	5.9	10.22
	♀	88	7.7-11.7	9.10	0.70	7.7	89	9.2-12.1	10.67	0.64	6.0	9.83
PM_1	Total	219	6.7-10.1	8.38	0.58	6.9	216	8.3-11.8	10.21	0.59	5.8	9.29
	♂	125	6.7-10.1	8.42	0.59	7.0	122	8.9-11.8	10.35	0.55	5.3	9.39
	♀	94	7.2-10.0	8.33	0.58	7.0	94	8.3-11.4	10.07	0.64	6.4	9.20
PM_2	Total	197	6.0- 9.8	7.50	0.59	7.9	194	7.3-12.2	10.27	0.58	5.6	8.88
	♂	115	6.0- 9.8	7.57	0.65	8.6	112	7.3-12.2	10.39	0.62	6.0	8.98
	♀	82	6.1- 8.4	7.44	0.49	6.6	82	8.9-11.5	10.15	0.53	5.2	8.78
		MANDIBULAR TEETH										
M_1	Total	128	9.9-13.2	11.24	0.50	4.4	128	9.2-12.0	10.35	0.52	5.0	10.79
	♂	64	10.4-13.2	11.36	0.51	4.5	64	9.3-12.0	10 47	0.50	4.8	10.92
	♀	64	9.9-12.2	11.12	0.49	4.4	64	9.2-11.8	10.24	0.54	5.3	10.68
M_2	Total	128	9.9-13.0	11.11	0.59	5.3	126	9.5-12.6	10.98	0.51	4.7	11.04
	♂	65	9.9-13.0	11.20	0.63	5.6	64	9.9-12.6	11.07	0.50	4.5	11.13
	♀	63	9.9-12.8	11.01	0.55	5.0	62	9.5-12.5	10.91	0.52	4.8	10.96
M_3	Total	117	9.2-12.4	10.50	0.63	6.0	117	8.8-12.1	10.38	0.55	5.3	10.40
	♂	61	9.2-12.4	10.54	0.65	6.2	61	9.6-12.1	10.58	0.57	5.4	10.56
	♀	56	9.3-11.8	10.46	0.61	5.8	56	8.8-11.3	10.22	0.53	5.2	10.34
PM_2	Total	128	7.0-10.0	8.24	0.54	6.5	128	7.3-11.1	9.04	0.62	6.9	8.59
	♂	65	7.0-10.0	8.31	0.61	7.4	65	7.5-11.1	9.15	0.67	7.3	8.73
	♀	63	7.0- 9.6	8.17	0.47	5.8	63	7.3-10.6	8.92	0.58	6.5	8.54

C. V. = $\frac{\text{S. D.}}{\text{Mean}} \times 100$. Module = $\frac{\text{Length} + \text{Breadth.}}{2}$ Length = Mesial Distal. Breadth = Buccal Lingual.

not differ in breadth, but M_3 is significantly less broad. The premolars do not differ in breadth.

The length of mandibular M_1 is slightly greater than M_2 and significantly greater than M_3. The breadth of M_2 is significantly greater than M_1 and M_3 which nearly equal each other in this diameter. This greater breadth of M_2 is the only dimensional feature manifested in chimpanzee molars that is reminiscent of the fossil and modern anthropoid characteristic of increased dimensions from M_1 to M_2 and M_3.

An examination of the coefficients of variation discloses M_1 as the least variable, and M_3 as most variable in the maxillary and mandibular molar classes respectively. Also, maxillary PM_2 is more variable than PM_1. These data are consistent with the findings of Dahlberg ('45) who applied Butler's ('39) "field" theory to the dentition. The following illustration from Dahlberg ('49, p. 139) will aid in understanding the concept. The symbol *S* denotes the tooth in each group

Maxillary	S	V	S	S	V	S	V	V
	I_1	I_2	C	PM_1	PM_2	M_1	M_2	M_3
Mandibular	I_1	I_2	C	PM_1	PM_2	M_1	M_2	M_3
	V	S	S	S	V	S	V	V

that is morphologically more stable in the expression and retention of ancestral patterns and the resistance to anomalous impositions. The other teeth in the respective tooth groups, indicated by the symbol *V*, are more variable. The greater the distance from the polar, or stable tooth, in a "field," the greater the variability. Dahlberg ('45) has indicated the validity of this theory in connection with the morphological features of human teeth.

To this theory is now added the support of metric data of the chimpanzee dentition. Figure 1 graphically illustrates the mean dimensions with their coefficients of variation in the molar and premolar teeth of Liberian chimpanzees. In general, length dimensions are more variable proceeding from M_1 to M_3 in both maxilla and mandible. A similar increase in the variability of the breadth diameters is noted in the maxilla from M_1 to M_3. An inconsistency with the "field" concept may be present in the coefficients of variation of the breadth diameters in mandibular M_1 and M_2, where the latter is slightly less variable. However, differences in variability of breadth diameters in mandibular molars from M_1 to M_3 are slight. The low coefficient of variation in mandibular M_2 may represent a persistence of the anthropoidal characteristic of the greater breadth of this tooth. Another inconsistency to the concept of

C. V. = $\frac{\text{S. D.}}{\text{Mean}} \times 100$. Module = $\frac{\text{Length} + \text{Breadth}}{2}$. Length = Mesial Distal. Breadth = Buccal Lingual.

variability is seen in the maxillary premolars, in which the breadth diameter of PM_1 is slightly more variable than that of PM_2, although the length of PM_2 is markedly more variable than PM_1.

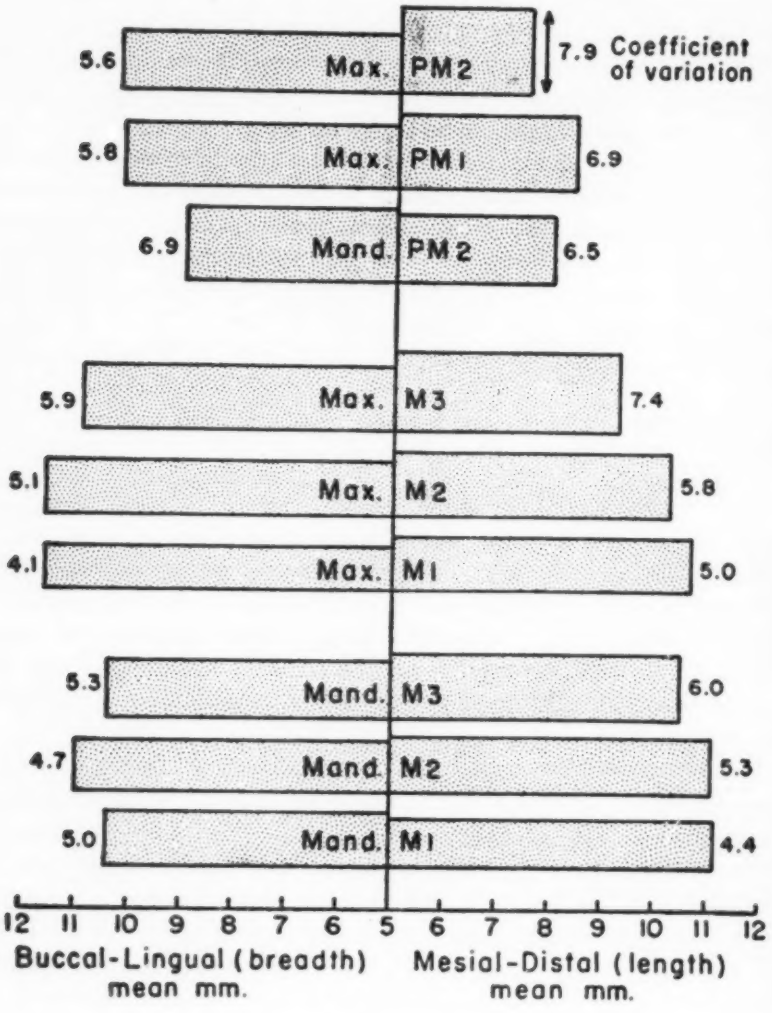


FIG. 1. MEAN DIMENSIONS AND COEFFICIENTS OF VARIATION OF LIBERIAN CHIMPANZEE TEETH.

It is generally agreed that the central tendencies indicated by mean values often obscure the variabilities around the means. For example.

it has just been demonstrated that the trend of the mean values is a decrease in dimensions from M_1 to M_3. However, there are many exceptions to this generality when the sequence within each molar group is noted. Table 2 lists these sequential variations. Neither the anthropoid progression $M_1 < M_2 < M_3$ nor the hominid regression $M_1 > M_2 > M_3$ alone predominates in a majority of the molar series. Several variations of both formulae appear in appreciable percentages. For example, $(M_1M_2)M_3$ and $M_2M_1M_3$ are almost equal in occurrence with $M_1M_2M_3$. Noteworthy are the relatively high percentages of $M_2(M_1M_3)$ and $M_2M_3M_1$ in the buccal-lingual diameters of mandibular molars of both male and female.

COMPARATIVE METRIC DATA

Senyurek's ('39) data on the orangutan and gorilla dentitions are selected for comparisons because of their completeness. Hrdlička ('26) published measurements of only the mandibular M_1 and M_2 of orangutan, gorilla and chimpanzee. Ashton and Zuckerman measured the dentitions of orangutan, gorilla and chimpanzee, but combined the dimensions of the unworn molars and premolars with those having undergone considerable attrition, so that the original tooth dimensions are obscured ('50). Gregory and Hellman ('26) confined their measurements to the mandibular molars and premolars, giving the mesial-distal and trigonid values.

Pedersen's data on East Greenland Eskimos ('49, pp. 80-81) and those of Nelson ('38, pp. 265-266) on the Pecos Indians are included for two reasons:

1. Both investigators have provided more statistically treated data than have most.
2. Pecos Indians and East Greenland Eskimos are similar to the Liberian chimpanzee in their homogeneity—having shared a common environment in relative isolation.

Pedersen provided sufficient data to permit our computing the coefficients of variation. In these computations, the values of right and left teeth were combined. The validity of this procedure has been previously stated (p. 241).

Nelson was forced to use samples sorted from loose teeth, so that sex groupings were not possible. In making our comparisons, we should consider Nelson's ('38, p. 278) statement to the effect that Pecos tooth dimensions are in the intermediate range of human populations. Campbell's data on the Australian Aboriginal dentition ('25, p. 17) are included because of their place at the top of the range of human teeth. Stein ('34, p. 1411) measured larger samples of American Whites than did G. V. Black. The latter did not indicate the size of his samples, but simply stated that a sufficient number of each variety of teeth were measured ('02, p. 14). Senyurek's *Homo sapiens* group provides dimensions on premolars and ranges of molars which have been omitted by Stein. Although Senyurek does not so state, it is implied that *Homo sapiens* refers to a group

TABLE 2

Dimensional Variations in the Sequence of Liberian Chimpanzee Teeth
(in terms of percentages)

	MAXILLARY				MANDIBULAR			
	Mesial-Distal		*Buccal-Lingual*		*Mesial-Distal*		*Buccal-Lingual*	
	♂	♀	♂	♀	♂	♀	♂	♀
*M_1 M_2 M_3	48	71	18	20	23	25	2	21
(M_1 M_2) M_3	19	20	35	40	30	23	2	16
M_2 M_1 M_3	9	2	23	16	12	21	18	9
M_2 (M_1 M_3)	3	0	9	10	0	4	32	36
M_1 (M_2 M_3)	9	3	6	5	18	7	0	0
(M_1 M_2 M_3)	5	2	6	6	9	14	7	7
M_2 M_3 M_1	2	0	1	0	2	2	25	16
(M_2 M_3) M_1	1	1	2	2	2	2	9	9
No. of Molar Groups Measured	110	85	107	82	57	57	57	56

Four additional variations in sequence were encountered, in remaining small percentages:

M_1 M_3 M_2 — (M_1 M_3) M_2
M_3 M_2 M_1 — M_3 M_1 M_2

* M_1 M_2 M_3 is the basic formula, indicating that M_1 is greater than M_2, M_2 greater than M_3. Order of dimension decrease reads from left to right in all formulae. Two or more teeth in parenthesis denote equal dimension. Since the error of measurement is 0.2 mm and each measurement is taken to 0.1 mm, differences in sequence in table 2 were recorded only when of the order of 0.3 mm or more. Any two diameters with a difference of 0.2 mm or less were considered as equal.

limited to White individuals. Senyurek's and Stein's data are similar to the values published by G. V. Black, and all of these are in the lower or lowest rank order of human tooth dimensions.

Due to the limitation of space, most comparative data are illustrated in graphs and figures, rather than recorded in tables. Figure 2 graphically summarizes the comparative dimensions of the molars and premolars of Liberian chimpanzee, orangutan, and human groups. The

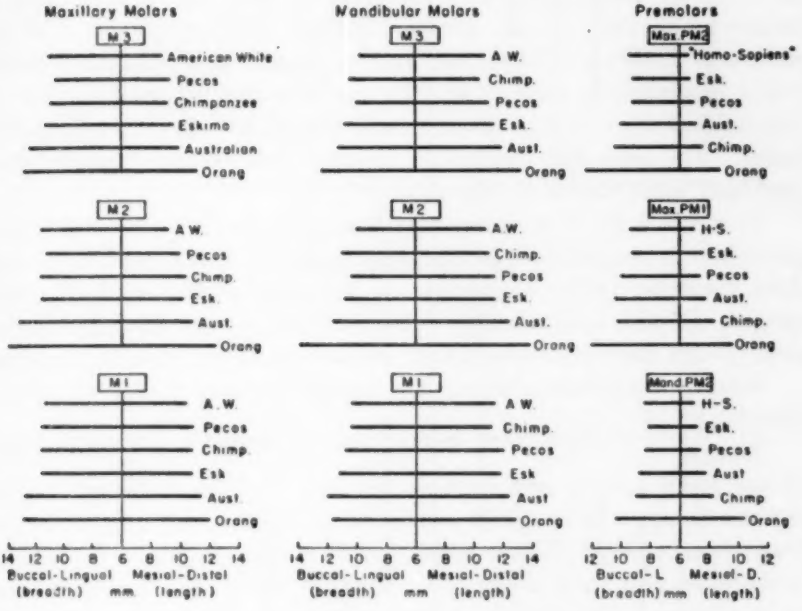


FIG. 2. MEAN DIMENSIONS OF CHIMPANZEE MOLARS AND PREMOLARS COMPARED TO THOSE OF ORANGUTAN AND HUMAN GROUPS

lines indicating mean values for breadth (on left) and length (on right) are arranged in rank order according to modules. The crown module is $\frac{\text{Length} + \text{Breadth}}{2}$. Pedersen, Hrdlička, Shaw, Nelson, and others agree that the crown module is an "expression of mass size" of the crown, although Pedersen ('49, p. 79) terms this a rather imperfect device. However, the crown module does give some indication of "relative" overall size rather than mass. It is quickly evident that the chimpanzee

molar mean dimensions fall well within human values, although their rank order differs slightly in mandibular and maxillary arrangement. The Liberian chimpanzee premolars suggest a central tendency just outside that of human premolars, although considerably closer to Australian than to orangutan.

Figure 3 is a graphic representation of the extent of the ranges of anthropoid and human molar dimensions. The comparisons are confined to maxillary M_1 and mandibular M_1 because these are the most stable molar teeth and would therefore be least likely to overlap in ranges among the various groups. Despite this, range values of the molars of Liberian chimpanzee, human groups, and orangutan consistently overlap with each other. In one case, the range of the buccal-lingual dimension of Australian mandibular M_1 is well within the gorilla range. The cross bars (figure 3) bisecting the vertical "range" lines represent mean values of dimensions.

In figure 4 the chimpanzee maxillary premolar alliance with human premolars is emphasized in the range values, which readily overlap. Also, the upper ranges of chimpanzee premolars overlap with orangutan ranges. Of added significance is the fact that overlap of ranges occurs even though there is great disparity in the sizes of the samples compared.

Most investigators compute the Length-Breadth Index of molars: $\frac{\text{Breadth} \times 100}{\text{Length}}$. This index is intended to disclose a general "shape" of the tooth and to provide a comparison of these "shapes" among various groups. Some fairly consistent generalizations may be derived from these indices.[2] Upper molar breath exceeds length, and the index is therefore of a value above 100. From M_1 to M_3 this index increases in orangutan, chimpanzee and human groups. The index of gorilla, however, is practically unchanged from M_1 to M_3. In mandibular molars, the index is generally below 100 (gorilla has the smallest mean index, 86% in M_1, Senyurek, '39), but a progression (or regression) of the index is absent in lower molars except for a slight tendency toward increase in M_2 in most groups. Senyurek (p. 121) states, "There is considerable variation in crown indices of the molars of anthropoids and the fact that the ranges of anthropoid indices overlap those of Hominid makes it impossible to use the crown index as a diagnostic criterion in classification of fossil [or other] specimen." The indices of

[2] The values of the indices discussed are taken from Senyurek's tables ('39, p. 112, p. 137).

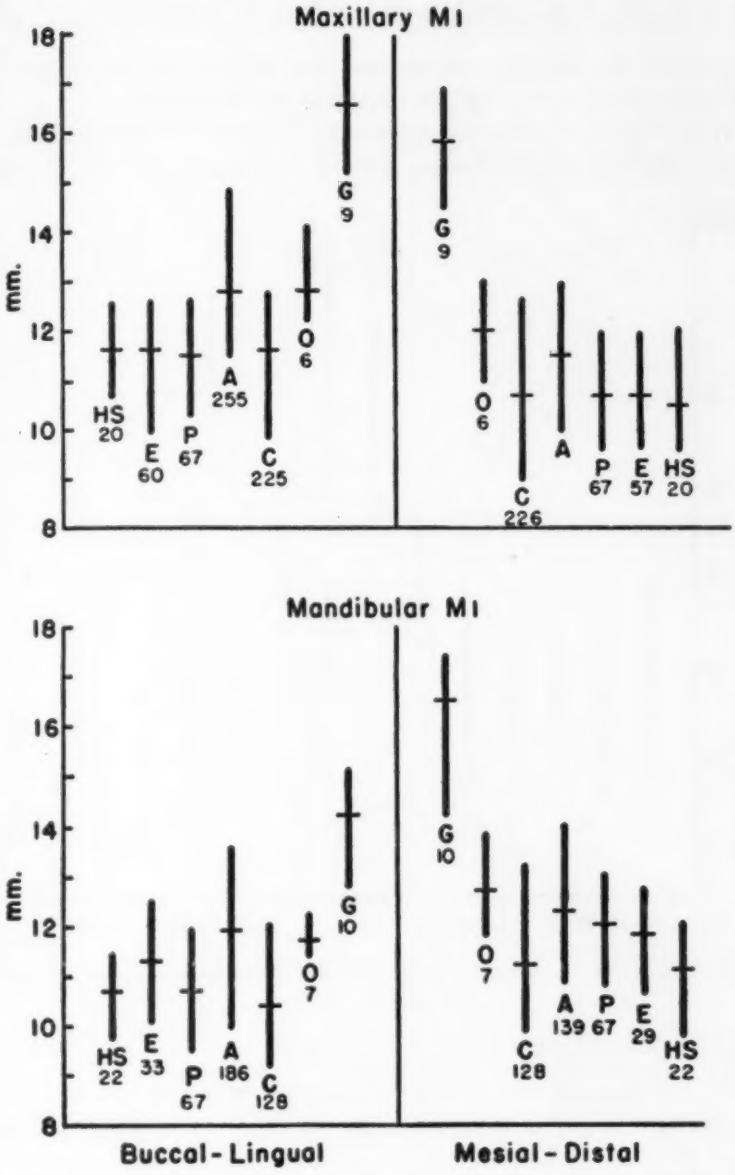


FIG. 3. RANGES OF DIMENSIONS OF FIRST MOLARS IN ANTHROPOID AND HUMAN GROUPS.

Vertical lines indicate extent of ranges.
Cross bars indicate mean values.
Numeral at bottom of each range indicates size of sample.

C = Chimpanzee (Liberian)
E = Eskimo (Pedersen)
P = Pecos Indians (Nelson)
A = Australian (Campbell)
O = Orangutan (Senyurek)
G = Gorilla (Senyurek)
HS = *Homo sapiens* (Senyurek)

Homo sapiens group included here in place of American Whites (figure 2) because ranges of latter not available.

the molars of Liberian chimpanzee are similar to the others just described and are therefore not tabulated or illustrated.

Since length and breadth indices do not seem to disclose differences between anthropoid and human molars, we suggest the use of another

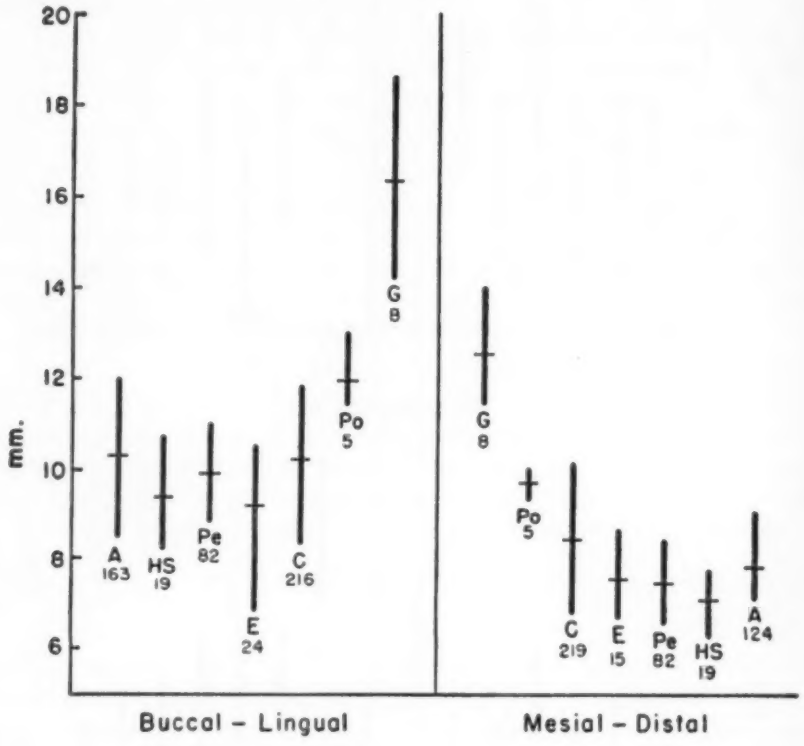


FIG. 4. RANGES OF DIMENSIONS OF MAXILLARY FIRST PREMOLARS IN ANTHROPOID AND HUMAN GROUPS.

Vertical lines indicate extent of ranges.
Cross bars indicate mean values.
Numeral at bottom of each range indicates size of sample.

Note: In this figure Po = orangutan (Senyurek) and Pe = Pecos Indians (Nelson).

device for comparing the changing "shapes" of teeth and the processes by which such changes are accomplished. This is utilized in table 3, where proportional changes in the dimensions of maxillary and mandibular M_2 and M_3 are expressed as percentages of the dimensions of the respective M_1 teeth. In this tabulation, the chimpanzee M_2 and M_3

TABLE 3

Decrease or Increase of Dimensions of M_2 and M_3
(expressed in percentage of maxillary and mandibular M_1 dimensions respectively)

		Gorilla		*Orangutan*		*Chimpanzee*		*Pecos*		*Eskimo*		*American White*	
		L	*B*	*L*	*B*	*L*	*B*	*L*	*B*	*L*	*B*	*L*	*B*
Maxillary	M_2	+ 8	+ 5	+4	+ 9	− 4	+1	− 8	−3	− 5	−1	−11	+2
	M_3	− 1	− 2	−6	+ 1	−13	−6	−12	−8	−10	−4	−14	−4
Mandibular	M_2	+10	+14	+9	+11	− 1	+6	− 5	−2	− 3	−3	− 5	−3
	M_3	+10	+12	+5	+6	− 7	0	− 8	−6	− 3	−4	− 4	−5

L = Length (Mesial-Distal).
B = Breadth (Buccal-Lingual).

follow more closely the trend of human molars in the percentages of dimensional decreases in terms of M_1. The one notable exception is an increase in the breadth of the chimpanzee mandibular M_2, another reminder that this is the only case where a chimpanzee molar dimensionally resembles other anthropoid molars. Gorilla and orangutan are unlike the chimpanzee in that, with the exception of the maxillary M_3, both dimensions of length and breadth increase from M_1 to M_3. The maxillary M_3 of gorilla is slightly smaller than its M_1 in both length and breadth. The orangutan maxillary M_3 undergoes appreciable decrease in length compared to M_1 but is about equal to M_1 in breadth. In maxillary M_2 and M_3 of the chimpanzee and human groups, the proportionate decreases are greater in length than in breadth. In the mandibular molars of the human group, the length and breadth modifications nearly keep pace with each other. The mandibular M_2 of the chimpanzee markedly increases in breadth over M_1, while the length diameters remain about equal. On the other hand, M_3 of the chimpanzee shows a large decrease in length and a stability of breadth with reference to M_1.

As in the case of length-breadth indices, the talonid-trigonid indices of anthropoids and human groups overlap in their ranges. Nevertheless, the ape molars seem to differ from human molars in the trends of these indices. In figure 5, the talonid-trigonid mean indices of human groups tend toward stability in all three molars, while in all the anthropoid groups these indices markedly decrease from M_1 to M_3. In other words, the talonid breadth decreases relative to trigonid breadth from M_1 to M_3. The chimpanzee mandibular molars in this case line up with those of the other anthropoids. In the human groups, the absolute values of mean indices for each of the three molars exceed those of the anthropoids except in the case of chimpanzee M_1, where the value is of human order. However, more and larger samples of human molars should be measured to determine the validity of the trends described.

Male and female values for Liberian chimpanzee and Eskimo have been combined to give a total coefficient of variation in each case. Over all male and female coefficients of Liberian chimpanzee teeth were tested for significant differences with negative results.

In the three groups compared in table 4, the trend of increasing variability from M_1 to M_3 in both maxilla and mandible, and from PM_1 to PM_2 in maxilla, is almost consistently maintained, reflecting the validity of Butler's field theory. This applies particularly to length

dimensions. Outstanding exceptions are the breadth coefficients in the premolars of all three groups, where there is greater variability in PM_1. Other inconsistencies are found in the Pecos group. These may be due to the difficulties Nelson encountered in sorting the teeth to be measured. M_1 and M_2 and even an occasional M_3 may have been interchanged. If

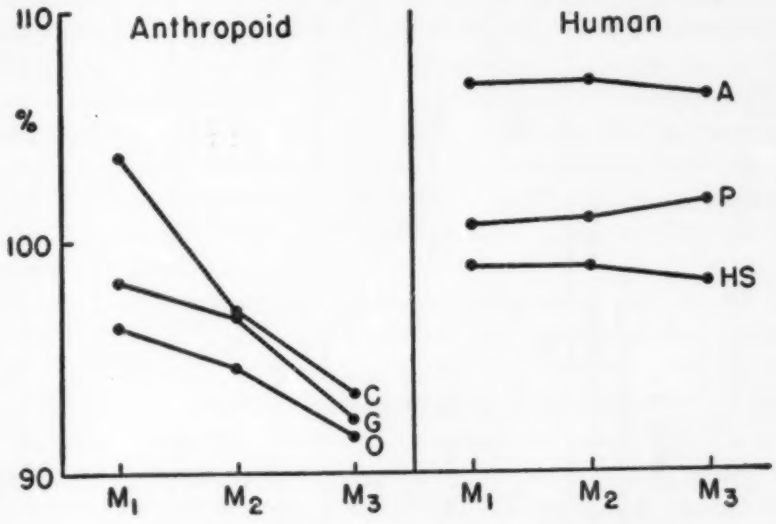


FIG. 5. TRIGONID-TALONID INDICES OF ANTHROPOID AND HUMAN MANDIBULAR MOLARS.

C = Chimpanzee (Liberian)
G = Gorilla (Senyurek)
O = Orangutan (Senyurek)
HS = *Homo sapiens* (Senyurek)
P = Pecos (Nelson)
A = Australian (Campbell)

The dots indicate mean trigonid-talonid indices: $\frac{\text{Talonid}}{\text{Trigonid}} \times 100$.

In anthropoid groups, the trigonid-talonid mean indices decrease from M_1 to M_3, resulting in increasingly tapered teeth. The trigonid-talonid mean indices in human groups tend toward uniformity from M_1 to M_3. For each of the three molars, respectively, the absolute mean values of trigonid-talonid indices in human groups exceed those of anthropoids except in the case of chimpanzee M_1.

this occurred a sufficient number of times, the expected variability trend could have been disturbed. The low coefficient in breadth of chimpanzee mandibular M_2 has been previously commented upon.

In general, the coefficients of maxillary teeth indicate a greater variability as contrasted to the corresponding mandibular teeth. This is more clear cut when the average coefficients are compared within each

TABLE 4

Coefficients of Variation Compared;
Liberian Chimpanzee, East Greenland Eskimo, Pecos Indian

	M_1		M_2		M_3		PM_1		PM_2		Av.
	*L	*B	L	B	L	B	L	B	L	B	
MAXILLARY TEETH											
Chimpanzee (Schuman Brace)	5.0	4.1	5.8	5.1	7.9	5.9	6.9	5.8	7.9	5.6	6.0
Eskimo (Pedersen)	5.0	4.6	5.1	5.7	8.9	6.8	6.5	6.1	7.6	5.8	6.2
Pecos (Nelson)	4.5	3.6	4.8	5.7	6.4	5.4	5.3	5.8	6.8	4.8	5.3
MANDIBULAR TEETH											
Chimpanzee	4.4	5.0	5.3	4.7	5.0	6.3	...	...	6.5	6.9	5.5
Eskimo	4.1	4.5	4.7	5.6	6.5	6.3	...	...	5.1	5.2	5.3
Pecos	4.6	4.4	4.0	4.5	5.9	5.3	...	...	6.2	6.0	5.1

*L = Length; B = Breadth.

of the three groups. Also it is seen that the average coefficient for Liberian chimpanzee molars and premolars (excluding the mandibular first premolar) is of the order of the two human groups, falling between East Greenland Eskimos and Pecos Indians for maxillary teeth and only slightly higher than either in the mandibular teeth. In line with Schreider's discussions ('53, p. 52) on the biometrics of physiology, we tested individual variations with reference to the error of measurement. For example, the smallest coefficient of variation (4.1%) in the Liberian chimpanzee dentition is that of the buccal-lingual diameter of maxillary M_1 (table 1). Since the error of measurement is 0.2 mm, the percentage for the particular diameter (11.6 mm) is 1.7% and therefore does not invalidate the 4.1% coefficient of variation. Similarly, in our remaining data, the percentage errors of measurement do not invalidate the true coefficients of variation.

Data on the chimpanzee canines are recorded in table 5. In spite of the striking differences in the cervical-incisal mean diameters between male and female in maxillary and mandibular canines of the Liberian chimpanzee, the range figures indicate male and female overlapping in both teeth. Therefore, to attempt an assessment of the sex of a chimpanzee skull, on the basis of the height of the canine alone, would often be a very questionable procedure. The sex difference in the mesial-distal diameter is not nearly as marked as the height differences; there is greater overlapping of mesial-distal ranges.

Figure 6 demonstrates that the canines of the chimpanzee are well outside of human range with one exception: the mesial-distal diameter ranges of the mandibular canines of female chimpanzee, Pecos Indians and *Homo sapiens* do overlap.

Table 6 consists of the mesial-distal diameters of Liberian chimpanzee incisors. The " field " concept is apparently adhered to in the maxillary incisors of the Liberian chimpanzee, in which the lateral incisors are the more variable. The mandibular central incisor of the male chimpanzee is also consistent with the expected reversal in variability—central incisor more variable than lateral incisor (see formula, p. 243). However, the female chimpanzee mandibular incisors seem to deviate from the " law " of variability in maintaining a greater variability in the lateral incisors. To offset this exception, it may be pointed out that the question of which mandibular incisor is more variable has never been settled. Additional data should serve to clarify the point.

TABLE 5

Dimensions and Variations of Canine Teeth
(Liberian Chimpanzee)

	Cervical Incisal					*Mesial Distal*					Height / Length
	N	Range	Mean	S. D.	C. V.	N	Range	Mean	S. D.	C. V.	
Maxillary											
Total	54	13.8-27.1	19.4	2.3	11.7	97	10.6-16.7	13.1	.93	7.1	147
♂	31	16.1-27.1	22.1	2.3	10.4	51	10.9-16.7	14.3	1.1	7.7	155
♀	23	13.8-18.5	15.9	1.2	7.5	46	10.6-13.2	11.8	.65	5.5	138
Mandibular											
Total	62	13.5-25.0	18.1	1.8	9.9	95	7.5-12.7	10.1	.75	7.4	179
♂	35	14.8-25.0	20.5	2.1	12.4	51	8.5-12.7	11.0	.8	7.3	186
♀	27	13.5-18.3	15.8	1.2	7.6	44	7.5-11.0	8.9	.62	7.0	177

Height = Cervical Incisal. Length = Mesial Distal.

TABLE 6

Mesial-Distal Diameters of the Incisors of the Liberan Chimpanzee

	Maxillary I_1					Maxillary I_2				
	No.	Range	Mean	S. D.	C. V.	No.	Range	Mean	S. D.	C. V.
♂	27	10.2-13.5	12.0	.75	6.3	25	8.5-10.9	9.7	.62	6.4
♀	22	11.1-13.5	12.0	.60	5.0	23	8.1-10.6	9.3	.56	6.0
Total	49	10.2-13.5	12.0	.69	5.8	48	8.1-10.9	9.5	.59	6.2
	Mandibular I_1					Mandibular I_2				
♂	27	7.1- 9.5	8.1	.60	7.4	25	8.0-10.0	9.1	.41	4.5
♀	26	7.3- 8.9	8.1	.40	4.9	21	7.9-10.0	8.8	.55	6.3
Total	53	7.1- 9.5	8.1	.53	6.5	46	7.9-10.0	9.0	.46	5.1

I_1 = Central Incisor. I_2 = Lateral Incisor.

In figure 7, it is seen that the mean values of mesial-distal diameters of the chimpanzee central incisors are much greater than the corresponding means found in human incisors. Also, the mesial-distal ranges

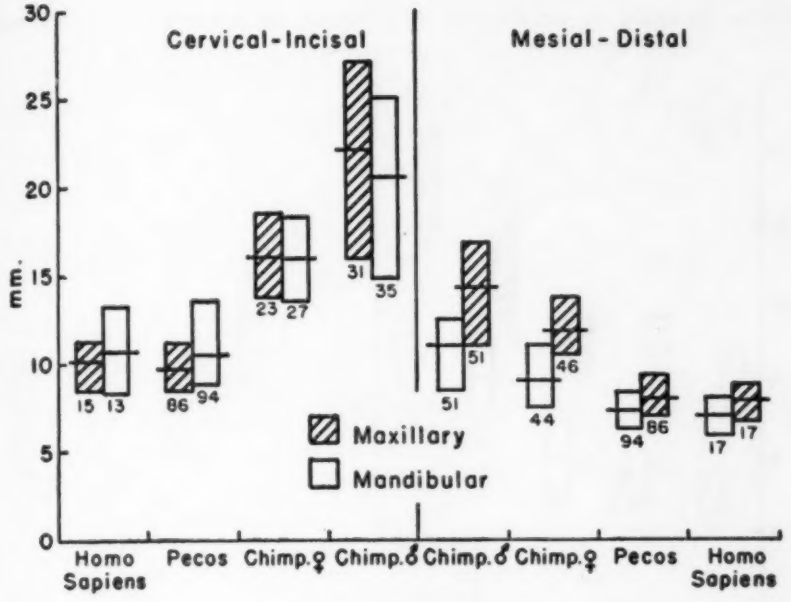


FIG. 6. MEAN VALUES AND RANGES OF CHIMPANZEE AND HUMAN CANINES.

Vertical bars indicate extent of ranges.
Cross lines indicate mean values.
Numeral at bottom of each bar indicates size of sample.

of chimpanzee central incisors are well beyond those of human central incisors. Again, the mean diameters and ranges of the chimpanzee lateral incisors exceed those of human groups with one exception: the ranges of maxillary lateral incisors of chimpanzee, Australian, and *Homo sapiens* overlap.

PART II

MORPHOLOGIC VARIATIONS

Mandibular Molars

Because of their evolutionary significance, there has been considerable interest in the various occlusal patterns of mandibular molars. The pattern ancestral to anthropoid and human molars was first observed

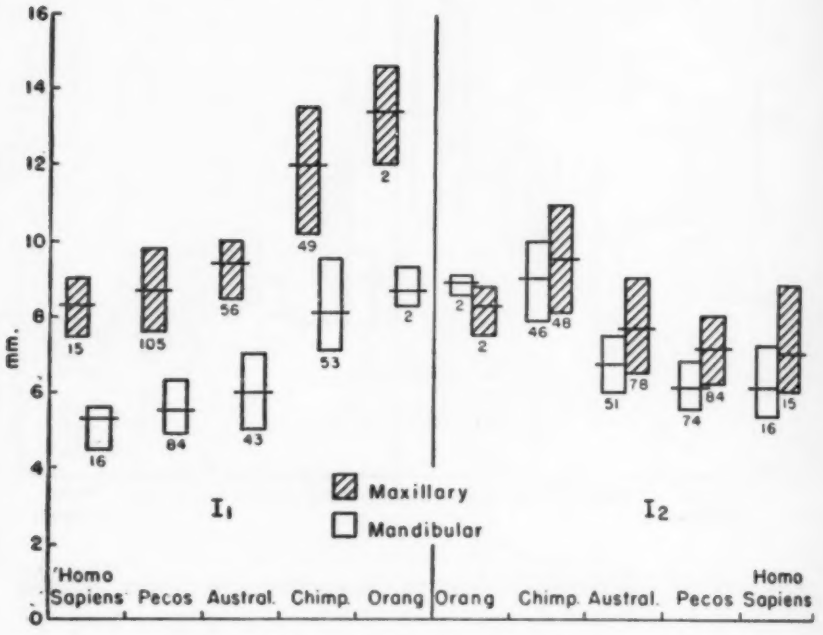


FIG. 7. MEAN VALUES AND RANGES OF MESIAL-DISTAL DIAMETERS OF ANTHROPOID AND HUMAN INCISORS.

Vertical bars indicate extent of ranges.
Cross lines indicate mean values.
Numeral at bottom of each bar indicates size of sample.

in the fossil ape, Dryopithecus (Gregory, '22). The Y5 pattern illustrated in figure 4 is considered to be typical of all the Dryopithecus molars, and any departure from this configuration supposedly represents a later phase in the evolution of molars. All of these features have been described in detail by Gregory and Hellman ('26, p. 105). For our purpose a brief description will suffice. Cusps 1, 2, 3, 4, 5 are proto-

conid, metaconid, hypoconid, entoconid, hypoconulid, respectively. In the traditional Dryopithecus Y5 pattern, where the three outer or buccal cusps, when viewed from the lingual, form a Y, cusps 3 and 2 are in contact (according to Gregory and Hellman) (figure 8). In the +5 pattern, the 3-2 cusp contact is replaced by the opposite contact, cusps 1-4. Gregory and Hellman have stated that "various intergradations

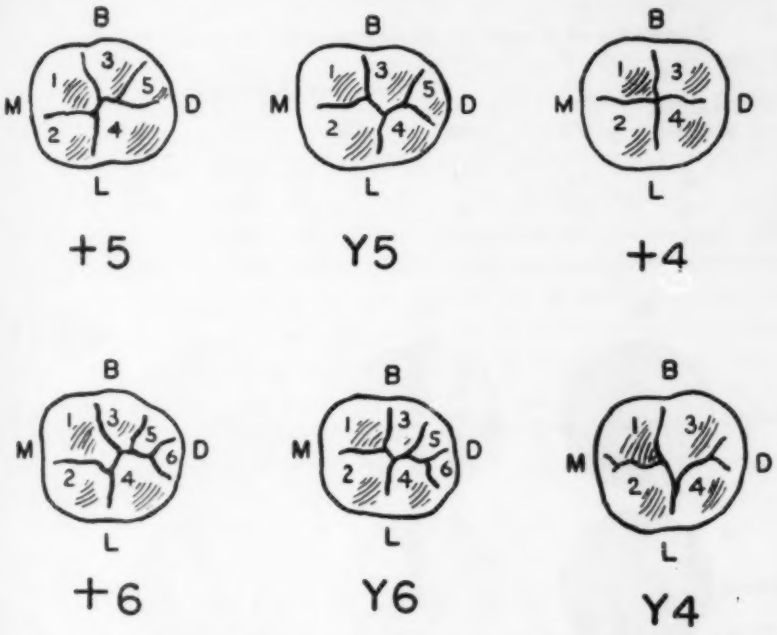


FIG. 8. MANDIBULAR MOLAR PATTERNS IN THE LIBERIAN CHIMPANZEE AND HUMAN DENTITION.

M—mesial, D—distal, B—buccal, L—lingual
1—protoconid, 2—metaconid, 3—hypoconid, 4—entoconid, 5—hypoconulid

The chief distinguishing feature between "Y" and "+" patterns is the relationship of cusps "3" and "2" to each other. In the "Y" pattern these are in contact, in the "+" pattern they are separated by cusps "1" and "4."

between the primitive Dryopithecus pattern with the complete Y and the typical plus-shaped human pattern have been observed . . ." We are in hearty agreement with this statement as a result of our efforts to analyze and categorize the various patterns. Too frequently a Y configuration is seen without the conventional cusp relationship that is supposed to accompany it.

In Y4 (figure 8) cusps 2 and 3 are in contact with 1 and 4 separated.

The various 6-cusp patterns in figure 8 follow the basic 5-cusp configuration with merely the sixth cusp added to the distal portion of the occlusal surface.

The distribution of mandibular molar occlusal patterns of the Liberian chimpanzee is seen in table 7. Since no appreciable sex differences

TABLE 7

Distribution of Mandibular Molar Patterns in Liberian Chimpanzee

	Total No. of Teeth	Percentage Distribution					
		Y5	+5	Y4	+4	Y6	+6
M_1	96	54	16	0	2	25	4
M_2	99	16	59	..	1	9	16
M_3	114	1	71	..	24	..	5

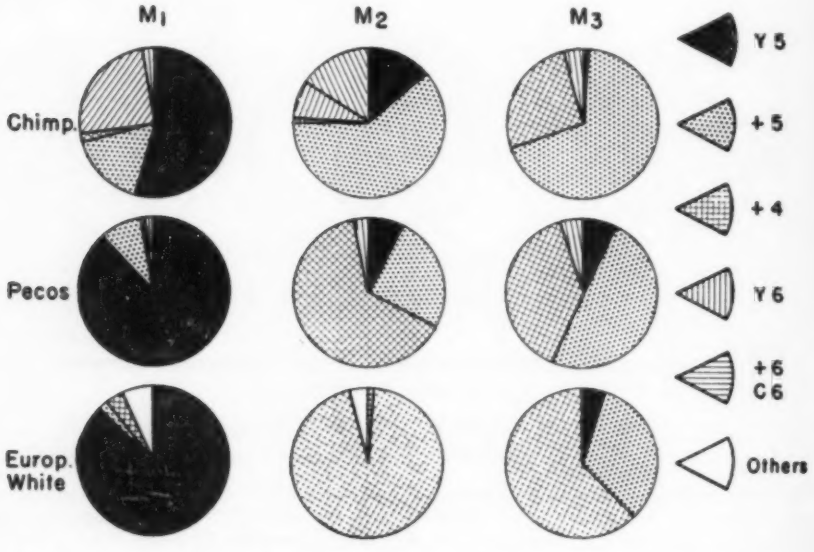


FIG. 9. MANDIBULAR MOLAR PATTERNS IN CHIMPANZEE, PECOS INDIANS AND EUROPEAN WHITES.

were observed, the male and female distributions were consolidated. The Y4 pattern does not seem to occur in the Liberian chimpanzee, and this parallels its low incidence in human molars.

The distribution of molar occlusal patterns in the Liberian chimpanzee is compared to those in human groups (figure 9). The

comparatively low incidence of the Y5 pattern in the chimpanzee first molar is contrary to the expectation that the primitive or ancestral pattern should occur at least as frequently as it does in man. However, 25% of chimpanzee M_1's show the Y6 pattern giving a combined (with 54% Y5) total of 79% Y configurations in M_1 and is therefore comparable to the Y incidence in human first molars. Other investigators either did not record 6-cusp teeth, or when they did, neglected to designate the pattern of these teeth.

Compared to the mandibular second molar of human dentition, the Liberian chimpanzee shows a persistence in the retention of a higher incidence of Y patterns (Y5 and Y6 combined). On the other hand, Pecos Indian and European White second molars present a high frequency of 4 cusps, while this trend in the chimpanzee is practically non-existent. The third molar of the chimpanzee tends to be 5-cusped more frequently than do human third molars, although 24% of chimpanzee M_3's have only 4 cusps. In general, as to occlusal pattern and the number of cusps, the mandibular molars of the Liberian chimpanzee retain the primitive or ancestral traits to a greater degree than do corresponding molars in Pecos Indians and European Whites. It is of interest that while Y patterns are practically non-existent in the chimpanzee M_3, the two human groups show appreciable percentages of this pattern in their M_3's.

Maxillary Molars

The reduction in size of the hypocone (disto-lingual cusp) of maxillary molars is considered to be another hallmark of the later phases of dentition evolution. In human molars, the hypocone is progressively reduced from M_1 to M_3 and very frequently is completely absent in M_3. The fate of the hypocone in chimpanzee molars is recorded in table 8. Five size grades are listed. In M_1 is found the highest percentage of large cusps; M_2 is dominated by medium cusps and M_3 by submedium cusps. Also M_1 contains the greatest percentage of smallest (slight) cusps. Three cusp maxillary molars were not observed. In several cases, the internal (mesio-lingual) cingulum extends distally onto the occlusal surface, making it difficult to distinguish such extensions from the presence or absence of a hypocone.

In figure 10 it is seen that the reduction in the size of the chimpanzee hypocone is of a trend similar to that of human molars; that is, reduction from M_1 to M_3.

TABLE 8

Reduction in Size of Hypocone from M_1 to M_3 in Liberian Chimpanzee

	Size	M_1 %	M_2 %	M_3 %
1	(slight)	0	1	19
2	(submedium)	1	10	52
3	(medium)	19	55	27
4	(large)	61	31	3
5	(very large)	19	3	0
	No. Teeth Observed	182	197	186

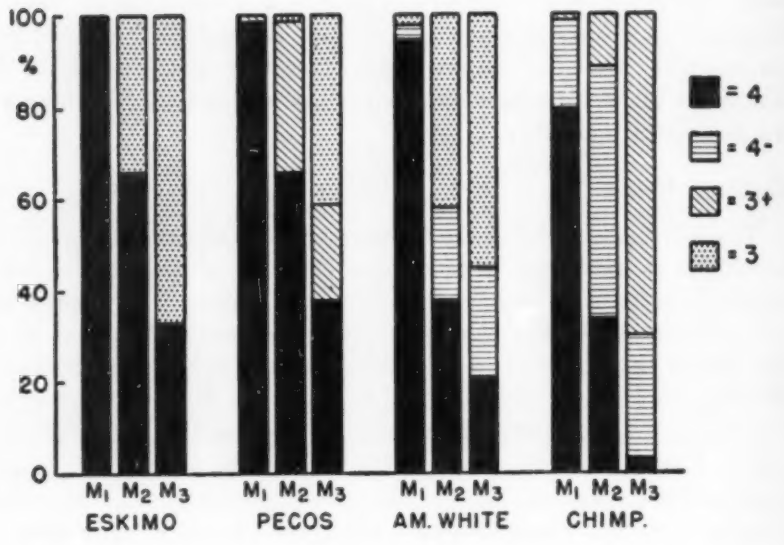


FIG. 10. REDUCTION IN SIZE OF HYPOCONE IN LIBERIAN CHIMPANZEE COMPARED WITH HUMAN GROUPS.

Size grades 5 and 4 (table 8) are combined to represent "4" in this illustration. Likewise, 3 (table 8) equals "4—"; 1 and 2 (table 8) equal "3+."

An anatomical feature observed in high frequency on the maxillary molars of the chimpanzee is the lingual cingulum. On M_1 this is usually confined to the lingual aspect of the protocone (mesio-lingual cusp). On M_2 this same cingulum is usually larger in all aspects and is extended more distally than it is in M_1. In M_3, the cingulum, while not of the absolute size found in M_2, is often relatively large compared

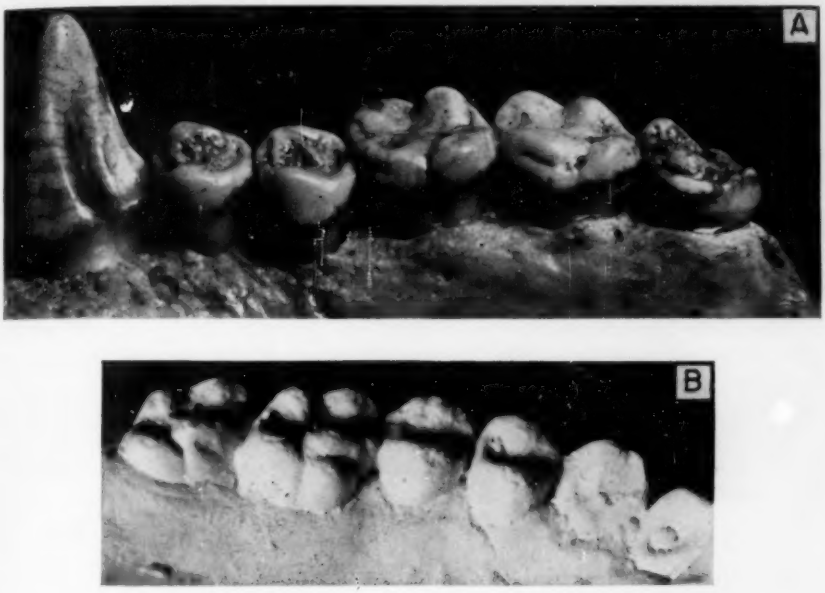


FIG. 11. THE MAXILLARY MOLAR CINGULUM OF CHIMPANZEE COMPARED WITH THE CARABELLI CUSP OF HUMAN DENTITIONS.

A. *Chimpanzee.* This illustrates the marked increase in size of the M_2 cingulum compared with M_1. In M_3, it appears that the cingulum is relatively large. Also, the cingulum here coalesces with the hypocone (disto-lingual cusp).

B. *American White.* The Carabelli cusp is much larger in M_1 than in M_2.

with the whole crown. Also in M_3, the cingulum may be extended even more distally than is the case in M_2, frequently to a point where it reaches the occlusal surface and seems to coalesce with the hypocone. The M_1 to M_3 progression of the cingulum is viewed in figure 11A. In human molars, a cusplet or cusp, known as the Carabelli tubercle, appears in the same location as does the cingulum of chimpanzee molars,

that is, on the lingual aspect of the mesio-lingual cusp. However, unlike the chimpanzee cingulum, the Carabelli structure is largest in M_1, occurs infrequently in M_2, and rarely in M_3 (figure 11B). Also it progressively decreases in size from M_1 to M_3 if present in two or more teeth. The foregoing descriptions suggest that the cingulum of the chimpanzee is unrelated to the Carabelli cusp. However, Bolk ('15) and other investigators have observed that there is a more distal location of the Carabelli cusp when it occurs on M_2, thus agreeing with the distal extension of the chimpanzee M_2 cingulum; Bolk also describes the "band-like" appearance of the Carabelli cusp on M_3 (possibly resembling a cingulum?). Gregory ('22, p. 454) concludes that "the presence of the external cingulum at the antero-internal corner of the first and second upper molars in primitive anthropoids . . . provides us with a starting point for the human line of specialization. . . ."

Appropriate to the cingulum-Carabelli controversy, to the scope of this paper in particular, and to our anthropological times in general, are a few lines from Gregory written in 1922 (p. 358):

> Whether or not the Piltdown jaw belongs with the skull, the fact remains that its contained lower molars are in many respects extremely like those of chimpanzees. But these, in turn, are closely related in pattern to human molars; and the whole Piltdown controversy serves to emphasize not only the fundamental agreements, but even the numerous special resemblances in structure of the jaws and teeth of chimpanzee and man.

In fully supporting this comment by Gregory, we are of the opinion that even the most astute odontologist could neither infallibly nor with a very high degree of consistency, distinguish between the molars of chimpanzee and man. The probability of such a distinction is further diminished when even a moderate degree of tooth wear has taken place. Observations by one of us (Schuman, unpublished data) reveals the fact that all of the varieties of patterns of tooth wear that occur in man also occur in chimpanzee and these range from flat to markedly oblique wear. These tooth wear patterns imply lateral movements of the mandible, and minimize the limiting factors usually attributed to anthropoid canines in this function. In addition to the metric and morphological similarities of the dentitions of man and chimpanzee, identical histological structures have been observed by Schuman and Sognnaes ('52).

All the observed variations in the dentition of the Liberian chimpanzee are the more significant because of the homogeneity of the group, living in isolation, and sharing a common environment.

DISCUSSION

With the exception of Pedersen ('49) and Nelson ('38), most investigators have provided insufficient data for comparisons with the metric variations occurring in the dentition of the Liberian chimpanzees. Therefore, in several instances, comparisons of variations are limited to the ranges of measurements. Schultz ('50) utilized ranges of indices to compare the limbs of man with those of other primates. A range composed of the mean, plus and minus two standard deviations, is probably a more valid method for comparing two or more series than is the comparison of their total ranges. Unfortunately, this device cannot be widely applied in the present study since standard deviations are available only in the Pecos Indian and East Greenland Eskimo groups. Where total ranges of measurements overlap only slightly, the use of the "limited" range (mean plus and minus two standard deviations) may serve to separate the ranges. A case in point is that of the mandibular canines of the Pecos Indian and female chimpanzee, where there is a slight overlap in the total ranges of mesial-distal diameters, 8.8-13.6 mm [8] and 13.5-18.3 mm respectively. This overlap is eliminated when the range of mean plus and minus two standard deviations is applied; the ranges are altered to 8.8-12.4 mm and 13.4-18.2 mm. However, in the East Greenland Eskimo, Pecos Indian, and Liberian chimpanzee, the total ranges of molar and premolar diameters overlap so extensively that the application of the limited ranges does not eliminate the overlapping.

The various illustrations of overlapping ranges of diameters in the dentitions from different species makes it apparent that the classification of a single tooth specimen on the basis of mean values and/or modules is a dubious procedure; it remains so even when sufficient data exist to produce statistically significant differences between the mean diameters of teeth from various groups. Another problem of classification is seen in the mandibular molars of the chimpanzee, which are of human order in their raw dimensions but which fall into anthropoid category when the trigonid-talonid indices are assayed (figure 5).

The breadth-length indices utilized by most investigators prove to be of little value, since the ranges of all groups (human and anthropoid) overlap, and differences in mean indices do not reflect the relative changes in breadth and length. These relative changes in breadth and

[8] Nelson ('38, p. 265).

length are disclosed in the procedure recorded in table 3, a procedure suggested as a replacement for length-breadth indices.

The continued use of the module as an index of "mass size" should be discouraged, since it not only does not represent mass size, but also tends to obscure the separate relative values of length and breadth diameters of teeth within and between groups.

SUMMARY

The metric and morphologic variations within the dentition of the Liberian chimpanzee have been demonstrated along with comparisons of these variations with those occurring in the dentitions of other groups, as follows:

1. *Ranges*: The ranges of chimpanzee molars and premolars overlap those of orangutan and human groups. The chimpanzee male and female canine ranges overlap; human and female chimpanzee mandibular canines tend to overlap in the mesial-distal diameter only. Incisors (except maxillary lateral incisors) of the chimpanzee are distinct in their ranges as contrasted to human incisors.

2. *Coefficients of Variation*: The coefficients of variation in Liberian chimpanzee dentition are similar in order to the coefficients of variation in Pecos Indian and East Greenland Eskimo dentitions. The maxillary teeth in all three groups seem to be more variable than their respective mandibular teeth.

3. *Butler's Field Concept*: Variation in the dentition of the Liberian chimpanzee support the concept as follows:

   a. Coefficients of variation increase with movement away from the polar tooth in each tooth group.
   b. Mandibular molar patterns in the Liberian chimpanzee tend to retain "ancestral Y" configurations in M_1 with a progressive decrease of these configurations in M_2 and M_3. Also, there is a tendency toward decrease in the number of cusps from M_1 to M_3.
   c. The decrease in the size of the hypocone from M_1 to M_3 parallels the decrease occurring in human molars.
   d. The cingulum (on the lingual aspect of the mesio-lingual cusp) increases either absolutely or relatively in size from M_1 to M_3. This may parallel (in reverse) the decrease in the incidence and/or size of the Carabelli cusp in human molars.

4. *Dimensional Variations in the Sequence of the Molar Teeth*:

Neither the human formula $M_1 > M_2 > M_3$ nor the anthropoid formula $M_1 < M_2 < M_3$ predominates in a majority of the molar series. Variations of both formulae appear in significantly high percentages.

The metric and morphologic features of the posterior dentition of the chimpanzee affiliate far more closely with man than with gorilla and orangutan.

The molars of contemporary chimpanzee exhibit ancestral patterns (dryopithecus Y configurations) to a degree similar to that occurred in contemporary man. This suggests a comparable evolutionary pattern for the posterior dentition of man and chimpanzee.

We are most grateful to Dr. Earnest A. Hooton, Dr. William L. Straus, Jr., and Dr. Maurice V. Stack for their invaluable aid in this study. This study was supported in part by the Division of Research Grants and Fellowships of the National Institute of Health, United States Public Health Service and also in part by the Wenner-Gren Foundation for Anthropological Research.

LITERATURE CITED

ASHTON, E. H., AND S. ZUCKERMAN 1950 Some quantitative dental characteristics of the chimpanzee, gorilla and orang-outang. Philosophical Transactions of the Royal Society of London. Series B, No. 616, Vol. 234: 471-484.

BLACK, G. V. 1902 Descriptive Anatomy of the Teeth. Fifth Edition. S. S. White Dental Mfg. Co., Philadelphia.

BOLK, L. 1915 Des Carabellische Hockerchen. Schweiz. Vierteljhrsschr. f. Zahnheilk., *25*: H. 2.

BUTLER, P. M. 1939 Studies of mammalian dentition. Differentiation of postcanine teeth. Proc. Zool. Soc. London, *109*: 1-36.

CAMPBELL, T. D. 1925 Dentition and palate of the Australian aboriginal. Univ. of Adelaide. Ph. D. Thesis.

DAHLBERG, A. A. 1945 The changing dentition of man. J. Amer. Dent. Assoc., *32*: 676-690.

—— 1949 The dentition of the American Indian. Papers on the Physical Anthropology of the American Indian. The Viking Fund, New York. Pp. 138-176.

GREGORY, W. K. 1922 The Origin and Evolution of the Human Dentition. Williams and Wilkins Co., Baltimore.

GREGORY, W. K. AND M. HELLMAN 1926 The Dentition of Dryopithecus and the origin of man. Anthrop. Papers of the Amer. Mus. of Nat. Hist., Vol. 28, Part I.

HRDLIČKA, A. 1923 Dimensions of the first and second lower molars with their bearing on the Piltdown jaw and man's phylogeny. Amer. J. Phys. Anthrop., *6*: 195-216.

NELSON, C. T. 1938 The teeth of the Indians of the Pecos Pueblo. Amer. J. Phys. Anthrop., *23*: 261-293.

PEDERSEN, P. O. 1949 The East Greenland Eskimo dentition. Meddelelser om Gronland, *142*. København.

SCHREIDER, E. 1953 Quelques problèmes préalables à toute recherche de biometric physiologique: Variations intraindividuelles, etc. Biologie, *12*: Nos. 1, 2, 3, 4.

SCHUMAN, E. L., AND R. F. SOGNNAES 1952 Surface texture and histologic structure of chimpanzee teeth; procedures and preliminary observations. Amer. J. Phys. Anthrop., n. s. *11*: 246.

SCHULTZ, A. 1950 The physical distinctions of man. Proc. Amer. Phil. Soc., *94*: No. 5.

SENYUREK, M. S. 1939 Evolution of human dentition. A metrical approach. Part II. Ph. D. Thesis, Peabody Museum of Amer. Arch. and Ethnol. Harvard University.

SHAW, J. C. MIDDLETON 1931 The teeth, the bony palate and the mandible in Bantu races of South Africa. John Bale Sons and Danielsson, London.

SNEDECOR, G. W. 1950 Statistical Methods. Iowa State College Press, Ames, Iowa.

STEIN, M. R., AND J. L. EPSTEIN 1934 The molar teeth of New Britain Melanesians. J. Amer. Dent. Assoc., *21*: 1409-1413.

TENTATIVE GENERALIZATIONS ON THE GROUPING BEHAVIOR OF NON-HUMAN PRIMATES *

BY C. R. CARPENTER

Department of Psychology

The Pennsylvania State University

INTRODUCTION

THE purpose of this paper is to formulate tentative generalizations about grouping behavior of non-human primates. The need is great for attempts to construct a conceptual system to give direction, form and significance both to collected data and to on-going research.

This paper is a condensed revision of a contribution to an international symposium held in Paris in 1950. The symposium was reported in a monograph entitled *The Structure and Physiology of Animal Societies.*

It may be premature to attempt to formulate generalizations and sketch the parameters of grouping behavior of primates. Available information is sketchy. The requirements of adequate sampling have not been applied to the selection and study of different types of orders, families, genera and species. Field investigations and experimentations have been integrated only to a very limited extent. Qualitative studies have not been balanced with quantitative studies on social interactions.

The generalizations which will be stated should be considered as hypotheses needing further proof or disproof. It is never premature in science to formulate hypotheses provided they are understood as such and not accepted as established principles.

* This paper is a summary of a more extensive study. See Carpenter '52.

BASIC ASSUMPTIONS

It may be useful to review several assumptions basic to comparative studies of social behavior. Although these assumptions are taken for granted by those of us who do research in the field, some are rejected, either explicitly or implicitly, by many of our colleagues. These assumptions are the following:

A. That the general principles of scientific methodology are eminently appropriate for investigating behavioral interactions of organisms, including grouping behavior, social stimuli and responses, social organization, and even complex cultural processes.

B. That a central task of comparative research on social behavior is to describe and measure, if possible, the central tendencies or commonalities of such behavior as well as its variabilities or differences.

C. That all levels of complexity of interactional social behavior operate within a tissue of ordered, interactional forces and deterministic energy systems.

D. That in the phylogenetic scale organisms and their behavior tend to become more complex from the so-called " lower " to " higher " forms, and that increasing complexity may result in differentiated " emergents."

E. That the analytic approach dealing with problems in an order varying from the simple to the complex is a justifiable scientific approach.

F. That a principal justification for investigating and striving to understand the social adaptations and adjustments of non-human primates is to add to the information and advance our understanding of the social adaptations and adjustments of man.

The following are assumptions which for us are untenable. Nevertheless, they *are* accepted, either implicitly or explicitly, by many of our colleagues, and in the interest of intellectual integrity we must argue their validity.

A. That the primate *Homo sapiens* differs so greatly from all other genera of the order Primates, especially on the level of complex social behavior, that investigations and data of non-human primates have no significant relevance to understanding the deter-

minants of human behavior or, conversely, that the similarities of the two are so great that identity can be assumed.

B. That the phenomena known as "mind," language, society, culture and "values" exist exclusively on the level of human evolution.

C. That explanatory systems can consist of dichotomous, over-simplified concepts such as heredity-environment, physical-mental, emotional-rational, implicit-overt, natural-supernatural, individual-social and animal-human.

D. That the predominantly important determinants of social adjustment operate in external situations or, conversely, that genetic determinants in the organism are of predominate importance in determining social behavior.

These and similar untenable assumptions have led to prevalent *homocentric delusions* which pictures man abstracted out of his biotic context, as dissociated from his supportative base of natural resources and as living and merely acting in response to the currents of "social" forces. Furthermore, the conflict of basic assumptions which we have outlined above has led to disassociations of the biological and social sciences and to the "foreign" languages of different academic disciplines. One example is the fantastic verbiage which has been developed by psychoanalyists and psychiatrists to describe sex behavior, aggression, and reaction to social controls of the individual.

Let us now attempt to formulate tentative generalizations for some of the major features of grouping behavior.

SPATIAL DISTRIBUTION

A basic approach to the study of grouping behavior in non-human primates is that of describing the objective, observable and perhaps measurable spatial distributions of populations and organized groups. Non-human primates are restricted in their geographic distribution and adaptations to climates and biotic environments of tropical and subtropical regions. Why? Apparently because they do not migrate, hibernate, store food nor build shelters which effectively protect them from weather. Thus, we may generalize (1) *that non-human primates lack adaptive and adjustive capabilities for coping with those degrees of climatic variations and fluctuations in food supply other than those variations typical of tropical and semi-tropical regions.*

Within geographic ranges and in population segments, organized groups of types which have been studied show strong tendencies to adjust to limited territories. These territories are occupied, possessed and defended against other organized groups of the same species. However, groups of other species or genera are tolerated within territories. The evidence seems to be adequate to support the generalization (2) *that organized groups of non-human primates adjust to limited territorial ranges and defend these territories against other organized groups of the same species.*

Within territories, organized groups arrange themselves in patterns of group scatter. Different genera exhibit different but characteristic grouping patterns. The average spatial arrangements of individuals to each other in a group, ignoring variations introduced by disturbed actions, would seem to express, or be indicators, of strengths of attachment, interdependence or probabilities of interactions among members. From this we may derive a third generalization (3) *that individuals in free-ranging organized groups deploy themselves in space in an inverse relation to the strength of positive interactional motivation and conditioning and in direct relation to the degree of negative motivation and conditioning.* This generalization could be transformed into an expression of interaction probabilities. Exceptions occur for fighting in which antagonism of some degrees results in close-in hostile behavior.

COMPOSITION OF GROUPS

Sufficient information is available to permit formulating several important generalizations about the composition of non-human primate groups. The first of this series is: (4) *that the sizes of groups in undisturbed populations varies within definable limits and around central grouping tendency characteristic of a genus.* This generalization indicates that the sizes of groups fluctuate within each species or genera and that there are size differences for different genera. The comparative research problem becomes that of determining what factors influence the number of animals in groups and what factors operate in various species or genera to produce inter-genera variabilities. Age of the organized group, reproductive rate, group division and population density are known to affect group sizes. The number of animals and their characteristics importantly affect the behavior of individuals and the group as a whole.

CENTRAL GROUPING TENDENCIES

Records of central grouping tendencies for different types provide additional descriptive information which can be compared for different types. The following are expressions of median groupings for three representative types:

Howlers

3 adult males + 7 adult females + 2 infants + 4 juveniles
+ unknown number of males living alone

Spider Monkeys

2 adult males + 4 adult females + 2 infants + 4 juveniles
+ extra group males living in groups

Gibbons

1 adult male + 1 adult female + 1 infant + 3 juveniles
both males and females living alone temporarily.

Confidence is high in the reliability of the expressions for howlers and gibbons but low for spider monkeys. Recently, recalculations on population data of howlers of Barro Colorado Island for 1935 and that published by Collias and Southwick ('52) show that percentages of different categories to total population in groups remain relatively stable even after marked reduction in the total population and the consequent reduction in the size of groups. These data lead to the fifth generalization: (5) *that proportions of different classes of animals in groups with respect to age and sex is more stable than the total size of groups.*

SOCIONOMIC SEX RATIO

In the non-human primate groups which have been studied, extra-group individuals have been observed. In most genera, these extra-group animals are males, but in gibbon populations both "solitary" males and females are observed. These animals apparently reflect differences in the ratios of adult males and adult females living within groups since in most there are fewer males than females. Thus, we come to a generalization on this intra-group socionomic ratio which seems to be a function of basic social adjustments. The relevant generalization is: (6) *that the composition and stability of primate groups is strongly affected by the relative balance of male with female sexual hungers and capacities and reciprocal satisfaction among adult members of groups.*

STATUSES OF INDIVIDUALS IN GROUPS

Status is an ordinal concept applicable to individuals arranged on the basis of behavioral data along a gradient scale or continuum. Individuals have status only relative to other individuals. The definition of social gradients of behavior and interactions within groups is one approach to describing the structure of groups. There are probably many such definable gradients, e. g., rights of access or possession, prestige or behavioral effects, spatial positioning "privilege" and dominance-subordinance. Of these the latter has been investigated most and is best known. The relevant generalization is: (7) *that in non-human primate groups there exist ordinal series of positions or definable continua or gradients which represent for individual animals, relative to others, the probabilities of occurrence of definable kinds of overt behavior.* And, for our purpose, the variously defined behavior of "dominance" may be sketched by the generalization (8) *that the probability of access to incentives appropriate to activated drives of interacting animals defines the dominance statuses of individuals.* Several subordinate facts are noteworthy: Dominance for a given individual, in a given group context, tends to be relatively constant; nevertheless variations occur in the drive strengths of interacting individuals. Also, a kind of *social summation* of statuses may occur when individuals are closely associated. Also, an individual may *derive* status from association with another or other individuals. In extreme cases, finally, and with few individuals, supreme, exclusive and generalized statuses may be attained. All statuses in primate groups must be continuously maintained. Status may be lost gradually or suddenly.

GROUP CONTROL

Organized groups have behavioral systems for regulating and controlling their actions. In the past these have been inadequately described by emphasizing for most types the anthropomorphic concept of "leaders." Therefore, another generalization is in order: (9) *that the control of a group is distributed among individuals and classes of individuals in direct proportion to the statuses of individuals or classes of individuals.* Control potentials are learned by group members and control is often exercised through signal or cue behavior associated with specific individuals and their actions.

INTEGRATION

Groups of non-human primates exhibit observable behavior which indicates varying degrees of group integration. Some of these indicators are the number and kinds of individuals which join or leave the groups, the variations in group scatter or spatial patterning, the amounts of intra-group conflict, degrees of concerted action, etc. Conceivably, the integration of groups is affected by both centripetal and centrifugal types of behavioral interactions. What then determines the direction and degrees of these "social movements"? This brings us to the tenth generalization: (10) *that the vector sums of the centripetal and centrifugal forces equal the degree of group cohesion or integration, and in turn, the drives, tensions or needs of individuals interacting with incentive behavior of other individuals both modify and stabilize the total network of interactions in the group.* Simply stated, many of the drives of each individual are satisfied, or reduced by interactions with other individuals. The interactions are reciprocal and this reciprocity of interaction principle is considered to be very fundamental in the dynamics of groupings. The principle refers to organism-behavior characteristics which can never be neglected in the study of social behavior however difficult the task of specifying and measuring the dimensions of these interactions.

At this point let us revert from considerations of groups as wholes to the basic elemental unit. In the study of complex groups it will often be necessary to limit observations or measurements and to provide for controls. This brings us to a methodological generalization: (11) *that the basic interactional unit is the reciprocal stimulus response interactions of one individual with another symbolized by* $O^1 \leftrightarrows O^2$. A definition of this generalized unit of study involves describing O^1 and O^2, defining the quality of behavior, describing or measuring interactional factors and effects and describing the context in which the animals act. It is believed that this unit can be systematically extended to cover the total number of paired interactional possibilities of a group which equals $\frac{N(N-1)}{2}$. Experimentation under controlled conditions using the $O^1 \leftrightarrows O^2$ unit has been fruitful and remains promising.

AUTONOMY OF GROUPS

Organized groups of non-human primates tend to be autonomous; they are capable of maintaining, regulating and controlling themselves largely independently of aid or assistance from other groups. However, they are only semi-closed, since there are exchanges of members from group to group, under some conditions, thus providing for "out-breeding." The relevant generalization is: (12) *that organized groups of non-human primates tend strongly to be autonomous, self-maintaining and regulating.* Such groups express resistance and hostility to other organized groups of the same but not different species (genera).

These propositions set the stage for a final generalization: (13) *that organized groups of a population of the same species in a limited region do not have supergroup social mechanisms.* Groups are not included in tribes, clans, communities, etc. as are found on the human level. Kinship relations are not operative and inbreeding is the rule rather than the exception to the normative behavior of non-human primates.

LITERATURE CITED

CARPENTER, C. R. 1952 Social Behavior of Non-human Primates. Structure et physiologie des sociétés animals, Colloques Internationaux du Centre National de la Recherche Scientifique, *34*: 227-246, Paris, Mars 1950.

COLLIAS, NICHOLAS, AND CHARLES SOUTHWICK 1952 A field study of population density and social organization in howling monkeys. Proc. Amer. Philosophical Soc., *96*: 143-156.

PROBLEMS OF MENTAL EVOLUTION IN THE PRIMATES

BY HENRY W. NISSEN

Yerkes Laboratories of Primate Biology and Yale University
Orange Park, Florida

THE inclusion in this symposium of four papers dealing with behavior is a measure of the increasing importance assigned to behavioral phenomena in their relevance for the general problem of evolution. This relevance, recognized since even before Darwin, still needs to be underscored. The fact that the theory of evolution as we know it today is founded primarily on structural evidence is understandable enough, since structures leave a record whereas physiological processes and behavior for the most part do not. It might well be that if we had a record of behavior as complete as the fossil record of structures, this would yield as convincing a body of evidence for evolution as does the latter. As a matter of fact, a study of the behaviors of living species alone—together with the paleontological evidence regarding the order in which these forms appeared—provides in itself a substantial basis for postulating a process of evolution. It is true, also, that here and there behavioral criteria have been found useful in supplementing structural evidence in problems of taxonomic classification (e. g. Lorenz, '37).

In the hierarchy of life sciences, psychology or the study of behavior occupies a rather unique position. On the one hand, it represents the most complex unit, the highest level of organization, dealt with by any of the so-called biological sciences. On the other hand, it represents the unit from which all the social sciences take their start. Among the sciences, therefore, psychology is a sort of two-way funnel into which the biological sciences converge and from which the social sciences diverge.

It happens, also, that scientists—all scientists—are individuals and primates. This makes it not only natural but inevitable that we should be egocentric and anthropocentric in our interests. The essence of the individual is his behavior, including his feelings, attitudes and strivings. His bones, muscles, and blood chemistry are in this respect secondary, being the conditions necessary for behavior. Psychology thus represents the most direct approach to what is of most immediate interest to man. And comparative psychology is concerned with the phylogenetic or historical basis of man's behavior.

More to the point in the present connection is this: that if we think of evolution as having a direction—this direction being a *post hoc* inference from observation and thus implying no guiding purpose—then this direction is most readily defined in terms of a trend in behavior. As we shall see, behavioral differences are especially striking within the order of primates. We of course assume that a trend in structural change—specifically change in the nervous system—underlies the behavioral trend, but as of now the former is even less clearly defined than is the latter. This statement is not necessarily inconsistent with one of the main points I wish to make today: that one of the weakest links in the sciences dealing with evolution, the one most needing to strengthen its facts and theoretical framework, is that dealing with behavior. I should also introduce here a word of explanation about what follows in this discussion. Of the 50-odd living genera of primates (Simpson, '45) only a very few have been studied to any extent in regard to behavior: man, chimpanzee, the macaques and cebus monkeys. Our discussion of behavior, therefore, cannot give anything like the extensive comparisons within the order as did some of the previous papers. We shall have to content ourselves with the grosser distinctions between the few aforementioned primates.

In a survey of behavior from ameba to man we find both similarities and differences, depending largely on the scale of observation used. In general, the similarities are expressed in terms of function or adaptive outcome. The differences are quantitative or refer to details of mechanisms which have more or less the same results. That is to say, the evolutionary development of behavior shows a continuity which parallels that of physical structures. There is, however, one possible exception. Whereas the physical differences between man and some of the other primates are no greater than those found at many points along the phylogenetic scale, the behavioral differences between *Homo sapiens* and

the living nonhuman primates exceed those found anywhere else. They are so striking that the possibility of a break in the continuum, of a qualitatively new emergent, may be and is widely entertained. Simpson ('49, p. 286) for instance, characterizes man as "fundamentally a new sort of animal" with a "new sort of evolution." The "new sort of evolution" refers, of course, to culture, or, as he puts it, "the inheritance of learning." The importance of culture as an offshoot of organic evolution, and with almost limitless possibilities of development, has been stressed by many writers. Few would deny that it is an almost uniquely human achievement. It is a social phenomenon in that we are all affected by culture and in varying degrees contribute to it. Nevertheless it is, in the last analysis, a product of the human individual; it has to be "invented" as well as used. It is in the characteristics of the individual, therefore, that we must seek its explanation. Simpson ('49, pp. 291-92) goes on to say that the human species "has properties unique to itself among all forms of life." These properties of the individual include especially "the accumulation of knowledge, . . . a sense of values, and the possibility of conscious choice." ('49, p. 290). As I shall try to show later, the differences in knowledge and in "a sense of values" are basically quantitative.

Let us consider first the chronically vexacious problem of consciousness. Is man the only conscious animal, or is he merely more conscious than others? Or could it be that some animals are more conscious than man? These are obviously hopeless questions. The only conciousness that we can observe directly is our own, personal awareness. And especially since Freud, we know that conscious content gives only a partial and highly prejudiced account of the factors actually determining behavior. In comparative psychology, certainly, we cannot use conscious processes as data. This fact has no implication for the question of whether animals are, or are not, conscious. Our best guess may be that consciousness is a quantitative rather than all-or-none phenomenon and that it appears in some degree in animals other than man. Having worked with chimpanzees for a number of years, I have no doubt that these animals are sometimes angry, resentful, jealous, remorseful, affectionate, happy or sad; that they have intentions and expectations which may be frustrated or satisfied. This conviction probably influences the design of my experiments but is almost worthless in reporting my results. Mentalistic terms are a convenient, short-hand way of designating and classifying various sorts of behavior, but they do not furnish any useable

data. The term "mental evolution" in the title of this paper was intended to convey the idea that most or all of those forms of behavior, which in us are accompanied by awareness, can be seen also in the higher nonhuman primates. Whether in them those behaviors are accompanied by awareness is irrelevant; the behaviors themselves, and their mechanisms, are legitimate material for comparative psychology and are pertinent to the general problem of evolution.

The phenomena to be considered in a phyletic comparison of behavior may be grouped into three classes: 1) the realm of cognitive or intellective functions—all those problem-solving capacities which we often lump under the term "intelligence"; 2) the emotional and motivational aspects of behavior; and 3) these first two classes in their social-cultural manifestations. In each of these fields evolutionary progression (or succession) has been characterized in various ill-defined ways. It is said that as we "go up" in the phyletic scale we find a greater range, diversity, and complexity of intelligent behavior; more flexibility or plasticity versus rigidity; increased learning capacity. Some intellectual functions, such as abstraction and symbolism, are usually ascribed only to the "highest" animals. The needs of the organism increase in number and complexity. Play, exploration and curiosity become more prominent as motivators of behavior. The forward reference of striving and planning encompasses longer periods of time. There is, in general, greater socialization, specialization and division of labor among individuals; and social organization becomes increasingly independent of genetic determination. This list could be greatly extended but is long enough to illustrate how vaguely phylogenetic differences in behavior are usually formulated. The first need, obviously, is the analysis of these gross descriptions into their components. To say that man differs from other primates in his capacity for tool-making and language is not very useful until we have identified the mechanisms or processes which produce these complex end-results.

Our problem is one of measurement: to measure the differences and similarities of behaviors exhibited at various phylogenetic levels. Before we can measure we need, first, axes or continua of variation, and second, units in terms of which differences along the axes may be described. In the physical world we have such axes as length and such units as inches. In psychology we have good measures of certain basic functions but as yet relatively few clearly defined dimensions of variation and units of measurement for the higher levels of behavior. In respect to

the basic or relatively simple functions, the measures indicate very little difference between the primate species which have been tested. Visual acuity, for instance, is almost the same in man and chimpanzee (Spence, '34); color vision is slightly better in man than in chimpanzee and rhesus monkeys (Grether, '39, '40). Simple reaction time—the speed with which an organism can respond to a signal—is the same for young chimpanzees and human children of comparable age (Forster, '35). In the speed of forming those uncomplicated associations known as classical conditioning, there appear to be no differences between the most primitive and the most highly developed animals (Razran, '33). In remembering a well-practiced task or association over long periods of time, the available data show no differences among the primates which have been tested (Nissen, '51a). Phylogenetic differences, and especially those critical for a comparison of the lower and higher primates, are evidently to be sought in what we loosely refer to as the "higher mental functions." And these functions, as I have indicated, are as yet imperfectly defined. I might say, parenthetically, that the same difficulty confronts the testers of human intelligence. For the most part their measures of mental age and IQ are based on unanalyzed end-products, with little knowledge of the functions which entered into the test-performances.

The difficulties of measurement, and also our earlier rough survey of phylogenetic differences, suggest a phrase which characterizes these changes: increasing complexity. This term is obviously descriptive rather than explanatory and is too broad to be useful unless the complexity is further specified. I suggest that complexity be defined in terms of the sheer number of factors which determine behavior. The number of determinants may increase both spatially and temporally. In the lowest organisms the most intense stimulus of the moment tends to govern the reaction. Later, the reaction is increasingly determined by a number of concomitant stimuli that influence each other by summation, inhibition, and so on. In vision, for instance, light intensity and direction govern the responses of the protista. In higher invertebrates, light distribution or patterning also becomes effective. The cumulative effects of previous experience become major factors in governing response to present stimulation, and this influence extends to more remote time. This temporal integration, I should point out, is a function of the individual. It is tempting to analogize and to say that the time-binding capacity of man extends to the race, via culture. But this is only an analogy. Education, imitation and so on are special ways of having

experience; the integration of those experiences is still a function of the individual.

A formal experiment may serve to illustrate the proposed dimension of increasing behavior determinants (Nissen, '51b). A chimpanzee is trained that choice of the larger of two square white plaques is rewarded, whereas choice of the smaller one is not rewarded. He then learns that if the two squares are black, the smaller one is correct. After these two habits are learned, he finds out that if the plaques are triangular instead of square, the previous relations are reversed; the smaller of the white triangles and the larger of the black triangles are positive. The problem is further complicated until the chimpanzee has to take into account 5 different factors or cues in order to make the right choice. This problem, which puts some strain on a human subject, was mastered by the chimpanzee. A similar experiment conducted by Noer and Harlow ('46) indicates that rhesus monkeys can respond to at least 4 cues. Rodents and carnivores have great difficulty when the number of essential cues exceeds two.

Since behavioral complexity is roughly correlated with phylogenetic level, we may ask whether, in back of this correlation, there is a more fundamental difference in cognitive mechanisms. The relative importance of genetic versus experiential determination would seem to constitute such a difference. This distinction, often referred to as "instinct versus intelligence," is especially clear if we compare, say, the insects and man. In the former, behavior seems to be largely a function of inherited mechanisms, whereas in the latter it is determined more by individual experience. The distinction is usually interpreted as a difference in the rigidity of stimulus-response connections; in the one case a certain response is innately elicited by a certain stimulus or situation, whereas in the other S-R connections are learned. This may constitute one of the differences but, I believe, only a minor one. More important is that in the "lower" animal the repertoire of perceptions is for the most part genetically fixed, whereas in the "higher" animals that repertoire is built up by or in experience. The instinct-guided animal is ready for its species-characteristic behavior almost as soon as it is born; the primate passes through an extended period of helpless infancy and childhood before it is ready for self-sufficient adult behavior. Evidence is accumulating that in chimpanzee as in man the principal learning going on during this time is the formation of perceptions, that is to say, the building up of a knowledge of the world, making sense out of what at

first is an undifferentiated confusion. I have suggested elsewhere (Nissen, '51a) that so-called play behavior provides the experiences which leads to perceptions and knowledge, and that this is why we see so much more play in the primates than in those animals which come equipped with ready-made perceptions, and more in young than in old animals. Experiments conducted at the Yerkes Laboratories with dark-reared infant chimpanzees indicate that the art of seeing, of perceiving contours and patterns, recognizing a milk bottle and the familiar attendant, is the result of prolonged learning or experience. The distinction between acquiring perceptions as contrasted with forming habits or S-R connections is important. The child has the perception of a door when he knows that it is a means of entrance and exit, a way to let in fresh air or to keep out the cold, and so on. He has a door-habit when he always slams the door shut. Perceptions are knowledge which can be used in forming habits or in acquiring other higher-order perceptions. Having learned to perceive squares, circles, triangles and so on, we may then, if we are one of the higher primates, acquire the perception—or as it is more commonly called, the concept—of form. The learning animals, therefore, can multiply their perceptions enormously, and this increase in the number of behavior determinants correspondingly increases the complexity of behavior. The instinct-guided animals, on the other hand, are stuck with their limited number of innately provided perceptions, which increase little with experience and which thus limit behavior to a lower degree of complexity.

In case there are any extreme environmentalists present today, it may be in order to point out here that man and the other learning animals have not actually escaped genetic determination. The potentialities for perception and conceptualization are inherited just as much as is eye-color, and those potentialities are limited in kind and number. With the right inheritance an individual may, under favorable conditions, acquire a great deal of knowledge, but, by definition, he will not become Superman. We are thus assured that experience will not make a man out of a monkey, although the opposite is alleged to occur sometimes.

In respect to innateness of behavior-determination, it is clear that the higher monkeys and apes stand a great deal closer to man than to most other mammals. The chimpanzee seems to have hardly any more instinctive modes of response than does man. Wild chimpanzees regularly build tree nests to sleep in at night, and these nests have a fairly uniform structure. There is pretty good evidence, however, that this

nest building is not instinctive, as in birds, but is, rather, transmitted by imitation or tuition from one generation to the next; it is, therefore, one of the very few items of behavior seen in these animals which may be classified as cultural. Mating behavior, which is highly instinctive in most mammals, is for the most part a matter of trial-and-error learning in the chimpanzee. One of the few behaviors of this ape which may be designated instinctive is grooming, or as it is often called, flea-picking. This appears in the captive-born chimpanzee when there has been no opportunity for imitation or tuition. The stimulus is a shiny object or small irregularity in any surface. In general, however, the perceptions of chimpanzees appear to be as much a product of experience as are those of man; the ape's potentialities are more limited, but certainly much greater than those of nonprimate mammals.

Limitation in respect to the kind of perceptions which an organism can learn is related to the amount of temporal integration involved. The perception of relations such as larger-smaller, lighter-heavier and so on are immediately given in a single experience. Other relations, such as "the middle one of 3, 5, or 7," "the odd one," or "the one which matches the sample" cannot be perceived in a single experience but come from observing the common element in a number of successive experiences. This is true likewise of concepts like "color" and "form." In the conditional matching problem (Nissen, Blum, and Blum, '49) the animal must choose the color-matching object when sign A is present, but must choose the form-matching object in the presence of sign B. Mastery of this problem clearly involves the percepts or concepts of form and color. Although nonhuman primates do solve this problem, it takes them a long time. A human subject can solve it much faster. This difference may be in part a function of the backlog of experience and education, relevant to the problem, which most nonhuman primates do not have when first confronted by the situation. In much larger part, I believe, the difference is a function of a hypothetical mechanism which increases enormously the capacity for temporal integration.

The facts which compel us to infer such a mechanism are the radical increase (a) in the speed with which associations are formed and reformed, especially those involving higher level relations or concepts, (b) in the facility with which general principles or laws are used as short-cuts to problem solution, and (c) in the number of factors or items which can be utilized in determining response. This mechanism, therefore, does not introduce a new or higher kind of mental functioning,

but it does increase greatly the efficiency with which certain functions, already present in nonhuman primates, are performed. That greater efficiency permits a pyramiding of percepts and concepts, each level building on top of that of lower complexity. Each level operates in two ways: (1) it makes possible the formation of concepts of still higher complexity, and (2) it facilitates the handling of lower level percepts. Problems which the chimpanzee solves by slow and laborious memorization, the human solves easily and quickly by applying a higher level formula or principle. Mathematics furnishes many good examples of this pyramiding process. The name we give to our inferred mechanism is unimportant; if the term had not been so uncritically misapplied in the past I should be inclined to call it a symbolic process. Certainly it is associated with and, in us finds its major expression in, language. It should be emphasized, however, that "language" is two separable things: (a) a method of communication, and (b) a tool or instrument of thinking. If one of these functions has developmental priority over the other, it would seem reasonable to suppose that the use of symbolic processes as an aid to the individual in thinking and problem solving preceded language as a means of communication in social intercourse. At any rate, according to this schema of cumulative pyraminding increasing complexity of behavior determination is in the first place a function of quantitative increase, but this involves new kinds, i. e., higher level, concepts.

If we analyze the process of logical thought, including the formation of concepts, we find that it reduces to three processes: the recognition of differences, the recognition of similarities or identities, and most important, a proper balance between these two. To take a simple example: in the conditional matching problem already referred to, the subject must respond to the differences among colors *or* among forms, but must also respond to the similarity of various colors as contrasted to forms. Over-emphasis on either similarity or difference interferes with solution. In respect to this balance or, as we may call it, sagacity,[1] the nonhuman primate tends to err on the side of over-responding to difference. In general, the chimpanzee classifies as a scatter-brained individual, very sensitive to difference or change, and unlike the obsessed individual who responds to the similarities between widely divergent

[1] This meaning of "sagacity" is consistent with, but more restricted and specific than, that found in the writings of William James (1890) and Hollingworth ('28).

phenomena. This ape is therefore the "scientific" rather than the "philosophical" type. The species difference in sagacity is, of course, a quantitative one.

I have taken so much time in discussing the cognitive side of behavior that the perhaps more spectacular differences in motivational-emotional aspects, and their expression in social phonomena, will have to be neglected. I shall have to content myself with a bald statement of the thesis that there are no fundamental or qualitative differences between the emotions and motivations of man and the other primates; that the very large and dramatic differences in the expression of emotions and in the organization of motivational hierarchies are secondary, deriving from the cognitive differences already discussed. What especially characterizes human motivation is not its initiating goals, but rather the indirection and complexity of its approach to those goals. With our superior capacity for temporal integration and our higher level concepts which enable us to foresee a series of causes and consequences, we can make long-range plans by which our ultimate goals are more efficiently approached. We are not restricted to an immediate striving towards the advantages of the moment.

Through complications introduced by social interaction and culture, most of our activities may appear unrelated to primary drives, but our more obvious goals are merely way-stations on the road to satisfying a relatively few simple but universal needs. As to Simpson's criterion of "a sense of values" for differentiating between man and the lower animals, I believe that no one who has had intimate acquaintance with the higher nonhuman primates will question that their actions are also guided by a delicately balanced system of values. The larger and stronger male chimpanzee deferring to his female companion in the division of food, even after the female is pregnant and no longer suitable as a sex partner—the animal "punishing" the misbehavior of his cagemate and in position to inflict serious injury, but contenting himself with merely nipping him painfully—the chimpanzee refusing to expose himself to the frustration of occasional failure in a difficult problem, although he could get a desirable tidbit 50% of the time by merely continuing to make a simple and easy response—these are but a few of many instances of a finely adjusted hierarchy of values. Like man, the chimpanzee has many values only indirectly related to primary needs, as for food, sex, and knowledge. But man recognizes in almost everything some relevance, however farfetched, to his basic needs, and his

system of values therefore has a greater numerical range and thus a greater complexity of interrelationships. Activities motivated by the primary drives involve the whole intricate organization of human economic and cultural life with the many subgoals which occupy most of our attention. Even the motives of altruism, ethical conduct and the like, are the expression of basic motivations, in us guided by superior intelligence, which we share with the other primates.

LITERATURE CITED

FORSTER, M. C. 1935 Temporal relations of behavior in chimpanzee and man as measured by reaction time. I. Simple reaction time. J. Comp. Psychol., *20*: 361-383.

GRETHER, W. F. 1939 Color vision and color blindness in monkeys. Comp. Psychol. Monogr., *15* (4): 1-38.

—— 1940 A comparison of human and chimpanzee spectral hue discrimination curves. J. Exp. Psychol., *26*: 394-403.

HOLLINGWORTH, H. L. 1928 Psychology; Its Facts and Principles. D. Appleton and Co., New York.

JAMES, W. 1890 The Principles of Psychology. Henry Holt and Co., New York.

LORENZ, K. 1937 Ueber die Bildung des Instinktbegriffs. Naturwissenschaften, *25*: 289-300, 307-318, 324-331.

NISSEN, H. W. 1951a Phylogentic comparison, in Handbook of Experimental Psychology (Ed. S. S. Stevens), John Wiley and Sons, New York.

—— 1951b Analysis of a complex conditional reaction in chimpanzee. J. Comp. Physiol. Psychol., *44*: 9-16.

NISSEN, H. W., JOSEPHINE S. BLUM, AND R. A. BLUM. 1949 Conditional matching behavior in chimpanzee. J. Comp. Physiol. Psychol., *42*: 339-356.

NOER, MARY C. AND H. F. HARLOW 1946 Discrimination of ambivalent cue stimuli by macaque monkeys. J. General Psychol., *34*: 165-177.

RAZRAN, G. H. S. 1933 Conditioned responses in animals other than dogs. Psychol. Bull., *30*: 261-324.

SIMPSON, G. G. 1945 The principles of classification and a classification of mammals. Bull. American Museum of Natural History, *85*, page 35.

—— 1949 The Meaning of Evolution. Yale University Press, New Haven, Conn.

SPENCE, K. W. 1934 Visual acuity and its relation to brightness in chimpanzee and man. J. Comp. Psychol., *18*: 333-361.

THE CULTURAL CAPACITY OF CHIMPANZEE [1]

BY KEITH J. HAYES AND CATHERINE HAYES

Yerkes Laboratories of Primate Biology, Inc.
Orange Park, Florida

THE problem with which we are here concerned has been referred to by Kroeber ('48, p. 69) as "the unknown organic basis of the faculty for culture." [2] What sequence of events in organic evolution was necessary to prepare our presumably anthropoid ancestors for the way of life that uniquely characterises man?

We have approached this question by way of the assumption that man's ancestry includes at some stage, a species which was physically and behaviorally similar to the modern chimpanzee—in a general way, if not in detail.[3] (This assumption is not entirely unreasonable, but

[1] The work reported here has been assisted by grants from the American Philosophical Society, The Samuel S. Fels Fund, and by research grant M669 from The National Institute of Mental Health, U. S. Public Health Service. Footnotes 2, 3, 4, and 6 have been added in response to comments made by W. L. Straus, Jr. in his "concluding remarks" on the symposium.

[2] We are surprised by Straus' comment that "culture" is virtually undefinable, especially in view of his recent statement ('53, p. 262) that culture "implies social inheritance from one generation to another," and that "man, or the genus *Homo*, may then be defined as an animal possessing a culture, for it is this feature that particularly distinguishes him from all other animals." Others use the term in the same way, without making an issue of its definition (e.g.: Kroeber, '48, p. 8, Dobzhansky and Ashley Montagu, '47, p. 587.) Moore and Lewis ('52) have discussed the operational definition of culture at some length; but their product differs from others primarily in its unfortunate interaction with the definition of "hominid." Brief definitions are poor substitutes for thorough discussions, which are plentiful in the literature, and which indicate that most anthropologists use the term "culture" consistently, and know what it means.

[3] This is perhaps ambiguous. We do not assume that man's ancestry includes a form which resembled the chimpanzee more closely than it did the orangutan or gorilla. We merely assume an ancestor of broadly "anthropoid" type, which was enough like the modern chimpanzee to make our study of the latter relevant.

its main virtue is convenience: chimpanzees are available for behavioral research.) We have attempted to estimate the extent to which characteristics essential for culture were already present in this hypothetical, chimpanzee-like ancestor.

Our procedure has involved the intensive study of Viki, a chimpanzee who has spent the first six years of her life in our home and has been treated as nearly as possible like a human child (Hayes, '51, Hayes and Hayes, '50). This approach is necessitated by the fact that the behavior of man or any other animal may be markedly influenced by experience—a fact which is seldom denied but which is, unfortunately, often overlooked in comparative psychology (Harlow,'49; Hebb, '49).

We have given special attention to our subject's social behavior, and particularly to her communicative ability—since communication is the primary prerequisite for culture. We have also been concerned with her

The chimpanzee provides a good "model" for our purpose: it has many of the characteristics that man's ancestors are presumed to have had, and it is not highly specialized, in the sense of being irrevocably committed to a narrow adaptive zone. (The chimpanzee is capable of a variety of modes of locomotion, and can utilize a variety of foods obtained in a variety of ways [Yerkes, '43, p. 15, Yerkes and Yerkes, '29, pp. 213-216].)

It is generally agreed that man's ancestry passed through a 400 gram brain stage and a 50 kilogram body weight stage. Most, though not all students (Straus, '49) consider it likely that man's ancestors were structurally adapted for brachiation, at one stage. One of the purposes of this investigation is to evaluate the possibility that an animal with these structural characteristics could have entered the human, or cultural, adaptive zone. If it could, we see no reason to doubt that it could subsequently have made whatever progressive adjustments this adaptive zone favored—even though such adjustments might involve reversal of earlier adjustments to other adaptive zones.

There is some reason to suppose that the African apes have already undergone considerable reversal of the brachiating specialization. Despite common belief (Straus, '49, Hooton, '42), the Hylobatidae are the only living apes that actually use brachiation as a usual or important mode of locomotion (Yerkes and Yerkes, '29, p. 537, Nissen, '31, p. 34). Although the other anthropoids, including chimpanzee, are "brachiators" in a structural sense, they show this adaptation in very attenuated form, as compared with the Hylobatidae. The large apes may reasonably be thought of as descendants of a siamang-like species, who have long since ceased to be selected for brachiation, and whose brachiating structure has been modified toward a more generally useful form. (This interpretation is supported by consideration of the laryngeal air-sac, which is prominent and possibly functional in the siamang, but small and almost certainly non-functional in the living African apes.)

use of implements, since tool-using is a prominent feature of all known cultures.[4]

It seems conceivable, a priori, that cultural capacity might have developed through evolutionary changes of three general types: 1. changes in gross anatomy, 2. development of special mental abilities, 3. changes in motivational makeup. We will examine each of these possibilities in some detail.

CHANGES IN GROSS ANATOMY

The hand. It might be supposed that considerable modification of the anthropoid hand would be needed to make it adequate for skillful tool using. However, our data do not support this hypothesis; our subject uses a great variety of tools, and she uses them skillfully and easily enough to be of considerable practical value to her (figs. 1 and 2).[5] The relative shortness of her thumb does not, despite common belief, prevent her grasping small objects between thumb and forefinger (fig. 3). We suspect that another peculiarity of the chimpanzee hand, less often mentioned in the literature, may cause more difficulty. This is the lack of dorsiflexion of the wrist (Straus, '40) which sometimes makes it hard to position a tool properly, after it has been grasped. However, this is not a really serious impediment to tool using. Functional plasticity tends to outweigh structural rigidity. If Viki's dexterity is greater than that observed in most other chimpanzees, the discrepancy is readily understandable in terms of the oft-neglected factor of experience. Most chimpanzees have much less opportunity to develop their manual skill than human children have. Also, it must be remembered that many of the tools we ask chimpanzees to use were designed specifically to fit human hands, and are ill-suited for use by chimpanzees. The chimpanzee hand performs rather poorly with our shears, for instance; but it would probably operate quite effectively with shears designed to fit it (Kroeber, '48, p. 68).

[4] Invention and construction of tools are important too, of course; however, one of the prime functions of culture is to relieve the average individual of much of the burden of creation, by allowing him to utilize the products of his more capable fellows—as pointed out, e.g., by Hooton ('42, p. xxxix). In particular, six-year-old children need not, and normally do not, invent or construct tools to a practically significant extent. For this reason we are postponing a detailed account of Viki's creative activities to a later and more appropriate date.

[5] Viki's use of tools is illustrated extensively in a 16 mm, silent film (Hayes and Hayes, '53).

FIG. 1. LIGHTING A CIGARETTE AT 6 YRS.
FIG. 2. TRYING TO PULL A LOOSE TOOTH WITH PLIERS AND MIRROR (6 YRS).

FIG. 3. HOLDING A CIGARETTE WITH GOOD THUMB OPPOSITION (6 YRS).
FIG. 4. CARRYING A HEAVY BOX AT 4 YRS.
FIG. 5. DIGGING WITH A SPOON AT 5 YRS.
FIG. 6. THROWING A TOY TO KNOCK DOWN A LURE AT 3 YRS.

Posture. It has been suggested that modification of the anthropoid posture was the first and most basic step in human evolution, since bipedal locomotion would be needed to free the hands for the use of tools (e.g. Washburn, '50). However, if evolution operates by selection, rather than by foresight, tool using must have appeared first. Only then could the intrinsically inefficient, bipedal mode of locomation be favored in selection (Bartholomew and Birdsell, '53, p. 482). We seriously doubt that pre-cultural tool using, on an individual basis, would be of sufficient importance to permit bipedalism, and we therefore suggest that cultural tool using appeared when posture was still of the anthropoid type. This seems entirely possible. Most of man's tool using occurs in a sitting position, or a stationary, standing position—neither of which is difficult for chimpanzees (figs. 5 and 6). So far as the transportation of implements is concerned, a chimpanzee can carry small objects in all four extremities while walking quadrupedally, and heavy objects can be carried in both arms, while walking upright—for short distances, at least (fig. 4).[6]

Speech organs. The anthropoid lungs, larynx, and mouth have commonly been considered adequate for the production of speech sounds. However, Kelemen ('48) has recently ascribed the absence of speech in chimpanzee to its laryngeal structure. We are not prepared to evaluate Keleman's anatomical study as such, but we can say with confidence that he is mistaken about its functional significance. It may be true, as he reports, that the chimpanzee larynx is more complex than man's; but it is not true that chimpanzee voice production is more complex than man's, and therefore useless for speech. Chimpanzee vocalization does not differ appreciably from ours in its use of inspired breath or double tones, and the chimpanzee's air sac is not involved in vocalization. Chimpanzees can and do produce a variety of vowel and consonant sounds.

Brain size. Controversy over the classification of extinct primates often centers around their cranial capacities. Unless the brain was

[6] Contrary to Straus's interpretation, these two paragraphs have not denied "morphological and physiological changes in [non-neural] parts of the body an important role in the evolution of human behavior." We *do* deny that changes of this type were prerequisite to the transition from anthropoid behavior to cultural behavior. The omission of certain changes might have led to "men" whose behavior, while quite different from ours, would still be cultural, and in this sense "human."

large enough, the creature presumably could not have been sufficiently "intelligent" to behave like a man, and must therefore have been an ape. We do not know, of course, just how large a brain is "large enough," though Keith ('48, p. 206) has boldly drawn the line at 750 cc. The matter is obscured by the vague manner in which the term "intelligence" is often used. However, if this word is defined operationally in one of the various possible ways, we still have no definite information about its relation to the size of the brain or any of its parts. In the absence of data we venture to speculate as follows: Such processes as forming or retaining an association, perceiving a relationship, drawing an inference, or generalizing a principle, should be relatively independent of sheer mass of tissue. We consider it likely that the quantity of brain is primarily related to a quantitative aspect of its function—specifically to its information handling capacity. One of the most distinctive tasks imposed upon the human brain by man's cultural way of life is the assimilation and storage of a tremendous amount of information. On the other hand, the chimpanzee's 400 gram brain seems to be fully capable of handling all the useful information likely to be encountered directly by the individual. From this point of view, an increase in the size of the anthropoid brain would be of no advantage to its possessor, so long as he continued to lead a non-cultural existence. We suggest the possibility that most of the fourfold increase in cranial capacity, from anthropoid to man, took place after the appearance of culture and language, and therefore after primate behavior had become essentially human.[7]

SPECIAL MENTAL ABILITIES

The second type of evolutionary change which may, conceivably, have led to the appearance of culture, is the development of complex patterning in the fine structure of the brain, which would provide special mental abilities not adequately developed at the anthropoid level. These micro-anatomical details would be inaccessible not only to paleontological methods, but also to present histological techniques, so this kind of structural evolution could be known only by inference from behavioral data (Lashley, '47).

[7] Thorndike ('27, p. 415) has suggested that the innate component of intelligence is nothing more than the number of potential associative bonds available in the brain. We have made one abortive attempt to deal with information capacity experimentally, but there is still considerable doubt whether this will ever be practical (Hayes, Thompson, and Hayes, '52).

This brings us to the question of whether chimpanzees are deficient, as compared with man, in their neurological capacity for behavior which may be characterized as, for instance, abstract, symbolic, conceptual, relational, insightful, or foresightful. These concepts appear to have their sources in the complex behavior (or introspection) of sophisticated humans. This may account for the difficulty of defining them in terms of experimental operations applicable to non-cultural, non-linguistic, and uneducated subjects (e. g., Seward, '48, p. 280).

Man does not display these "higher mental functions" in a vacuum, but only in the context of skills and information which have been acquired through experience. A primate who has not acquired the same skills and information can hardly be expected to display these functions in the same form as man. If a primate's background of experience is sufficiently restricted, he may fail to display any "higher functions" in any form whatever—simply because of his lack of skills and information and regardless of the detailed structure of his brain. There have been only a few experimental studies which bear directly on this question, but they tend to support the hypothesis that "higher mental abilities" are acquired rather than inherited.

Tasks which involve the integration of events separated by an interval of time are sometimes said to require special "symbolic processes," and it is known that such tasks are extremely difficult for naive chimpanzees (Hallowell, '50, p. 165; Yerkes, '43, p. 188). Several studies have shown, however, that this difficulty may be eliminated by prior experience with simple discrimination-learning problems (Harlow, '44; Hayes and Thompson, '53; Riesen, '40).

It was once possible to suppose that learning by observation, as contrasted with direct experience, depended on some faculty which was confined primarily to man. Here again, however, an adequate background of experience has been found to make such learning very easy for other primates (Harlow, '44; Hayes and Hayes, '52).

In short, when the factor of experience is considered, there is no clear evidence that chimpanzees are deficient in any hypothetical, higher mental faculties. Furthermore, it may be questioned whether these special abilities actually exist, as such, even in man. We are inclined to favor Thorndike's hypothesis that "in their deeper nature the higher forms of intellectual operation are identical with mere association or connection forming, depending upon the same sort of physiological connections but requiring *many more of them*." (Thorndike et al., '27,

p. 415). We suggest that the "higher mental functions" observed in man are more nearly results of culture than causes of it.

MOTIVATIONAL MAKEUP

The third and last type of evolutionary development concerns the neural mechanisms which cause an animal to engage in various kinds of activity (Harlow, '53). These mechanisms are presumably micro-anatomical and inaccessible to direct observation but may be inferred from behavior. We are not particularly interested in the drives which cause an animal to eat, drink, and reproduce, but rather in the play drives—the innate tendencies toward behavior which serves no immediate, practical purpose. Such behavior has survival value because it provides opportunity for the acquisition of skills and information which may later be useful in the solution of practical problems. To avoid any irrelevant connotations of the word "play" (Beach, '45; Schlosberg, '47) and to indicate explicitly the significance of this phenomenon, we offer the alternative term, "experience-producing drives."

Cultural living, as we know it, requires an adequate background of experience in at least two broad areas: mechanical and social. The first is essential to the technological aspect of culture and the second to communication and cooperative enterprise.

Mechanical play. The chimpanzee resembles man very closely in mechanical interest. Our subject, Viki, spends a large part of her time playing with tools, toys, and household equipment, as well as with more primitive materials, such as sand, sticks, and water. This extensive mechanical play, coupled with the dexterity mentioned earlier, permits the chimpanzee to develop a very respectable amount of mechanical ability. It is our belief that no further evolution would be necessary to prepare the chimpanzee for the tool-using side of cultural life.

Social and communicative play. Chimpanzees also resemble man quite closely in preference for social play. Viki likes simple games which involve tickling, wrestling, chasing, and teasing; and it seems likely that such communicative ability as she has was acquired largely in the course of such play. However, she is markedly deficient in one type of drive which is very prominent in man—the drive toward specifically communicative and linguistic play.

This type of play appears as babbling in the human child, early in the first year of life, and provides extensive practice in the motor skills

of producing and combining speech sounds. During the next few years, after the child has learned the elements of speech, he takes great interest in learning new words—most of which have no practical value for him at the time, though they may be useful later. For the rest of the child's life, a large proportion of his speech satisfies no more immediate, practical need than that for self expression.

In the infant chimpanzee, however, vocal play is almost completely absent. During her first five months, Viki babbled enough to show that her vocal apparatus was capable of producing a variety of vowel and consonant sounds; however, she did much less of this than human infants do, and the activity did not persist nearly so long (Hayes, '51, p. 63).

After their first year, many chimpanzees engage in a type of sound-producing play which is somewhat similar to babbling; however, the sounds are produced by mouth movements only, without use of the larynx, and usually without use of the lungs. Some of these sounds closely resemble the "clicks" which form a part of certain human languages. Viki has produced only six of these sounds, and has shown no tendency to combine them in groups. They could thus provide only a very limited potential vocabulary.

Viki readily imitates our production of her mouth sounds and learns meanings which we assign to them. She can thus ask for a drink by saying "ch" (with the German pronunciation, as in *Ich*), or for a cigarette by saying "tsk," or for a ride in the car by clicking her teeth together. However, unlike the human child who has just begun to speak, Viki uses her words only for the practical purpose of getting what she wants. She does not engage in purely sociable conversation, or egocentric expression. She does not even use her words for practical purposes, if she can show us what she wants without them. When she wants a cup of cocoa, for instance, she silently leads us to the kitchen and hands us the ingredients. Only if we refuse to be led and stubbornly ask, "What do you want?" does she say "ch."[8]

We suggest that the most important step in the evolution of modern man from an anthropoid ancestor was an increase in the experience-producing drives relevant to the skills of communication. Others have hypothesised that apes do not talk because they have nothing to say (Kroeber, '28, p. 329). This seems to us like an inadequate reason—

[8] Some of Viki's vocal behavior is illustrated in a 16 mm. sound film (Hayes and Hayes, '50).

it does not keep people from talking. Furthermore, we have found that Viki often does have things to say. We contend that apes do not talk because unlike man, they have no inclination to talk when there is nothing to be said.

We have, in the past, suggested that chimpanzees may be innately deficient in some neurological mechanism which provides the capacity to learn language (Hayes, '51, p. 66). We still consider it conceivable that if a chimpanzee and a human child both had the same language experience, the chimpanzee might learn much less language. However, we now recognize that such speculation is meaningless, so far as available operations are concerned. It is impossible to coerce a chimpanzee into the kind and amount of language practice that the human child gets spontaneously. Since the known difference in motivation accounts for the observed difference in attainment, there is no point in postulating an unknowable difference in capacity.

COMMUNICATION AND EARLY CULTURE

The simple beginnings of culture would require only a little skill in communication—perhaps about as much as chimpanzees already have (Kroeber, '48, p. 223). It is important, in this connection, to note the difference between the invention and use of tools, on the one hand, and tool culture on the other. The importance of communication increases as the probability of an invention decreases. Invention of the wooden club, or the stone-used-as-a-missile, would probably occur in a large majority of isolated, individual chimpanzees, under appropriate circumstances, and would thus be independent of culture. The stone-tipped spear, however, would probably be invented very seldom, and would be available to a whole population, in successive generations, only if the methods of manufacture and use could be communicated. The chimpanzee's ability to learn by imitation would appear to make this possible—at least for simple tools and techniques.[9]

Another function of communication in culture is the facilitation of cooperative enterprise. Chimpanzees are capable of considerable communication which could serve for directing, instructing, commanding, or soliciting. Crawford ('37) has demonstrated cooperative behavior in the setting of a laboratory problem, and Viki commonly displays it spontaneously. She often requests our help with things which she cannot do, or is forbidden to do, or afraid to do, by herself.

[9] Viki's imitative ability is illustrated in a 16 mm, silent film (Hayes and Hayes, '52a).

The first method she used was the simple one of leading us where she wanted us to go. More recently, she places our hands on the objects she wants us to manipulate and often moves our hands in a manner suggesting the action to be performed. For instance, if she wants to go outside, she leads us to the drawer where the door key is kept and places our hand on the drawer pull. If we don't open it promptly, she gives our wrist a tug. When the drawer is open, she puts our hand to the key, and when we grasp it, she moves our hand to the key hole. If we continue to lag, she moves our hand till the key enters the key hole and finally twists our wrist to indicate the unlocking movement. (She knows how to unlock the door for herself, of course, but is not permitted to.)

Viki makes relatively little use of gestures of the hand alone, without contacting an object or person. She often points to things she wants, when they are near by and could be touched if that were allowed; but she seldom points to the door across the room, for instance, though she responds appropriately when we do so. She uses movements of her own hands to indicate an activity only rarely—as in the case where she wanted to help with the ironing but was forbidden to touch the iron. She moved her empty hand back and forth above the ironing board, apparently to show what she wanted.

This kind of communication may be said to involve "iconic signs," whose meanings are related in an obvious and logical way to their physical character. We have observed some behavior in Viki which suggests that chimpanzees may readily convert such signs into "symbols," whose meanings have an essentially arbitrary relationship to their physical character. When Viki was very young, we never took her for a ride in the car without taking some spare diapers along. As a result, she invented the device of asking for a ride by bringing us a handful of diapers from the bathroom. Later, she no longer wore diapers, but there were still some in the bathroom, and she still brought them out when she wanted a ride. When we eventually disposed of the non-functional diaper supply, Viki asked for a ride by running into the bathroom and coming out with a handful of Kleenex tissues—which bore only a faint resemblance to diapers. These tissues had never had any direct connection with rides, and by this time Viki had quite likely forgotten how the whole thing started. Except for its history, this would now appear to be communication by means of an arbitrary convention developed by the chimpanzee.

Viki commonly employs a particular type of vocalization in combination with her non-linguistic communication. This is a hoarse "ah," which serves to attract attention, and to indicate "asking," in a very general sense. We have observed a few other chimpanzees using this sound in the same way; but there appear to be very large individual differences in the ease with which it is produced. Some seem to do it spontaneously, while others fail to do it even with extensive training. This sound, unlike the chimpanzee's vocal expressions of emotion, is produced at will (Hayes, '51, p. 66) and could, conceivably, provide the starting point for development of spoken language.

We estimate that chimpanzees are capable of enough communication to permit several kinds of cooperative enterprise which might be typical of very primitive culture. An individual could go and get one or more others and bring them to a place where there was something to be done: a heavy load to be transported, a large animal to be attacked, or a good supply of fruit to be picked. If the nature of the task were not immediately apparent to the newcomer, he might be shown what was wanted. If he did not understand the technique to be used, he could ask for a demonstration. If he were reluctant to work, he might be coerced.

Chimpanzees could probably communicate well enough for some kinds of organized, group hunting: they might, for instance, be able to surround a herd of animals and stampede them over a cliff. We doubt, however, that they could arrange for certain individuals to wait in ambush while others drove the quarry to them. Their communication would probably be inadequate to deal with events remote in time or space.

If chimpanzees have this much cultural capacity, the question naturally arises, "Why don't they have culture?" There are several possible answers. One is that perhaps they do have some. We know relatively little about chimpanzee behavior in the wild (Nissen, '31) and cultural factors may well be involved in some of it. Another possibility is that culture appears only in the presence of excess capacity. Or it may depend on some unrecognized factors which we have not considered.

However, we tend to prefer the hypothesis that chimpanzees lack culture because they are adequately adapted to their environment without it (Nissen, '31, p. 104). Their mortality is probably due primarily to infectious disease (Schultz, '50, p. 51) and would not be reduced by

the techniques of a primitive culture. Food shortage, predators, or a rigorous climate could be combatted by simple cultural means; but these do not appear to be important factors in chimpanzee survival.

CONCLUSION

In summary, we hypothesize that modern man evolved from an anthropoid ancestor by way of the following sequence of events.

1. Due to migration or changing climate, a population of anthropoids encountered an environment in which cultural behavior had greater survival value than it has in the ecology of present anthropoid species. (This probably involved a shift from vegetable to animal food, which would present no serious difficulty. Viki eats a considerable amount of eggs, fish, and meat, including small lizards which she catches.)

2. In response to the new environmental pressure, a simple, nonlinguistic culture developed, which provided primitive tools and techniques for obtaining food, or protection from predators or climate.

3. In this cultural setting, language acquired a value it did not have before and began to develop on the foundation of a few sounds such as chimpanzees are able to use. With the appearance of language, selection occurred in favor of individuals with strong drives toward vocal and linguistic play, so that successive generations learned more language, and learned it more easily.

4. Finally, as the linguistic culture became more complex, larger information capacity became advantageous, and selection for large brains began. This selection probably operated on the growth pattern, producing a rather generalized fetalization (Keith, '48, p. 197; Schultz, '50, p. 46), with mature brain size as the basis of selection, and jaw size, head balance, etc., as incidental, correlated features.

It will be noted that the much discussed change in posture does not appear in this behaviorally oriented schema. The recent discovery of the pelves of South African ape-men (Broom, '50; Dart, '49) suggests that bipedal locomotion preceded brain enlargement in the evolution of man. However, it does not follow that upright posture was the first or most basic step in human evolution (Washburn, '50). The present analysis shows that it is a secondary character of only moderate importance. We agree with Kroeber's suggestion ('48, p. 68) that it could have been omitted completely, without seriously altering the basic outlines of human evolution.

LITERATURE CITED

BARTHOLOMEW, G. A., JR. AND J. B. BIRDSELL 1953 Ecology and the protohominids. Am. Anthrop., *55*: 481-498.

BEACH, F. A. 1945 Current concepts of play in animals. Amer. Nat., *79*: 523-541.

BROOM, R. AND J. T. ROBINSON 1950 Notes on the pelves of the fossil ape-men. Am. J. Phys. Anthrop., n. s. *8*: 489-494.

CRAWFORD, M. P. 1937 The cooperative solving of problems by young chimpanzees. Comp. Psychol. Monog., *14*, No. 68.

DART, R. A. 1949 Innominate fragments of *Australopithecus prometheus*. Am. J. Phys. Anthrop., n. s. 7: 301-333.

DOBZHANSKY, T. AND M. F. ASHLEY MONTAGU 1947 Natural selection and the mental capacities of mankind. Science, *105*: 587-590.

HALLOWELL, A. I. 1950 Personality structure and the evolution of man. Am. Anthrop., *52*: 159-173.

HARLOW, H. F. 1944 Studies in discrimination learning by monkeys: II. Discrimination learning without primary reinforcement. J. Gen. Psychol., *30*: 13-21.

——— 1949 The formation of learning sets. Psychol. Rev., *56*: 51-65.

——— 1953 Mice, monkeys, men, and motives. Psychol. Rev., *60*: 23-32.

HAYES, C. 1951 The Ape in Our House. Harper, New York.

HAYES, K. J. AND C. HAYES 1950 Vocalization and Speech in Chimpanzees, (16 mm, sound film.) Psychological Cinema Register, State College, Pa.

——— 1951 The intellectual development of a home-raised chimpanzee. Proc. Amer. Phil. Soc., *95*: 105-109.

——— 1952a Imitation in a home-raised chimpanzee. (16 mm, silent film.) Psychological Cinema Register, State College, Pa.

——— 1952b Imitation in a home-raised chimpanzee. J. Comp. Physiol. Psychol., *45*: 450-459.

——— 1953 The mechanical interest and ability of a home-raised chimpanzee. (16 mm, silent film.) Psychological Cinema Register, State College, Pa.

HAYES, K. J. AND R. THOMPSON 1953 Non-spatial delayed response to trial-unique stimuli in sophisticated chimpanzees. J. Comp. Physiol. Psychol., *46*: 498-500.

HAYES, K. J., R. THOMPSON AND C. HAYES 1953 Concurrent discrimination learning in chimpanzees. J. Comp. Physiol. Psychol., *46*: 105-107.

HEBB, D. O. 1949 The Organization of Behavior. Wiley, New York.

HOOTON, E. 1942 Man's Poor Relations. Doubleday, New York.

KEITH, A. 1948 A New Theory of Human Evolution. Watts & Co., London.

KELEMEN, G. 1948 The anatomical basis of phonation in the chimpanzee. J. Morphol., *82*: 229-256 (reprinted in Yearbook Phys. Anthrop., 1948, *4*: 153-180.)

KROEBER, A. L. 1928 Sub-human cultural beginnings. Quart. Rev. Biol., *3*: 325-342.

——— 1948 Anthropology, Harcourt Brace, N. Y.

LASHLEY, K. S. 1947 Structural variation in the nervous system in relation to behavior. Psychol. Rev., *54*: 325-334.

MOORE, O. K. AND D. J. LEWIS 1952 Learning theory and culture. Psychol. Rev., *59*: 380-388.

NISSEN, H. W. 1931 A field study of the chimpanzee. Comp. Psychol. Monog., *8*, No. 1.

RIESEN, A. H. 1940 Delayed reward in discrimination learning by chimpanzees. Comp. Psychol. Monog., *15*, No. 5.

SCHLOSBERG, H. 1947 The concept of play. Psychol. Rev., *54*: 229-231.

SCHULTZ, A. H. 1950 The specializations of man and his place among the catarrhine primates. Cold Spring Harbor Symposium, *15*: 37-53.

SEWARD, J. P. 1948 The sign of a symbol: a reply to Professor Allport. Psychol. Rev., *55*: 277-296.

STRAUS, W. L., JR. 1940 The posture of the great ape hand in locomotion and its phylogentic implications. Am. J. Phys. Anthrop., *27*: 199-207.

——— 1949 The riddle of man's ancestry. Quart. Rev. Biol., *24*: 200-223.

——— 1953 in TAX, S. (Ed.) An Appraisal of Anthropology Today. Univ. of Chicago Press.

THORNDIKE, E. L., E. BREGMAN, M. COBB AND E. WOODYARD 1927(?) The Measurement of Intelligence. Bureau of Publications, Teacher's College, Columbia Univ., N. Y.

WASHBURN, S. L. 1950 The analysis of primate evolution with particular reference to the origin of man. Cold Spring Harbor Symp., *15*: 67-77.

YERKES, R. M. 1943 Chimpanzees. Yale Univ. Press, New Haven.

YERKES, R. M. AND A. YERKES 1929 The Great Apes. Yale Univ. Press, New Haven.

CLOSING REMARKS

BY WILLIAM L. STRAUS, JR.

Laboratory of Physical Anthropology
The Johns Hopkins University

I BELIEVE that I am correct in stating that the peak of research on the nonhuman primates in this century was reached during its third and fourth decades. During the last fifteen or more years, however, the output of such studies has fallen off to a marked degree. The reason for this I do not know. Perhaps it is due to the war. Whatever the reason, however, the number of workers now actively engaged in primate research is almost pitifully small. The response evoked by this symposium leads me to hope that it may signal the beginning of a revival; for, although I admit to something more than a slight prejudice, I know of no aspect of anthropology that is likely to yield richer dividends to the investigator.

I am glad to note that Dr. Hooton agrees in essence with what I said at last year's Wenner-Gren international symposium about the present status of our knowledge of primates and about the important gaps that remain to be filled. He has, however, stated the case for extensive and intensive studies of nonhuman primates far more eloquently and more effectively than I possibly can.

I heartily endorse his statement about the pressing need for a broad and sound knowledge of nonhuman primates when reconstructing and interpreting the fossil remains of man and other primates. I would go even further, however—and I am sure that he will agree with me—and stress the imperative need of comparing fossils with large series of existing primates, utilizing biostatistical methods. There has been far too much reliance on that more facile method which a former mentor of mine used to call "anatomical appreciation." I know that I may be stepping on tender toes when I say this; nevertheless, I believe that too

much of what has been written about the Australopithecines falls into the latter category. And many studies of primate teeth, as Dr. Hooton has rightfully emphasized, furnish yet another important example.

Dr. Hooton has also emphasized the paucity, indeed the virtual absence, of genetic studies of nonhuman primates—studies that would, with little doubt, help elucidate some of the problems of human evolution. The obstacles to such studies are of course great, but so would be the rewards. The cooperation of primatologists, geneticists, and directors of zoological parks could scarcely fail to reap a rich harvest.

The paleontological papers of Dr. Jepsen and Dr. Patterson cannot help but impress upon us the important fact that the geological history of the primates is an extremely long one. As Dr. Jepsen has noted, only three of the living mammalian orders—the marsupials, the insectivores, and the carnivores—have, in our present knowledge, longer histories. Man is a terminal product of some 65 million years of primate evolution, and if we are really to understand him, we must take due cognizance of what has gone before. In this, as will again be noted later, Dr. Davis and myself see eye to eye. The whole gamut of primate evolution, from the early prosimians of the North American Paleocene onward, has undoubtedly left its mark on man as we know him today. In the past—indeed, even at the present time—too many students of human evolution have focussed their attention too closely or even exclusively on those animals that appear to stand nearest to man—that is, on the anthropoid apes, and particularly on the great apes—with resulting myopia and scotomata. The consequences of such a limited outlook have become all too evident in some evolutionary controversies. Although the geological history of the primates exhibits many irritating gaps, some of them are gradually being filled in. Indeed, certain recent discoveries have shed new light upon man's history: light that is in some respects quite unexpected in its nature. Yet many important problems of primate evolution remain for elucidation. To give but an incomplete list, there are the relationship of the tupaioids to the lemuroids and tarsioids, the question of a tarsioid origin of the simian primates, the history of the platyrrhines, the evolutionary relationships of the existing catarrhine groups, and, last but not least, the nature and the zoological position of the Australopithecines.

Some of these problems have been discussed by Dr. Patterson. He has made it clear that paleontology cannot yet speak with authority on the taxonomy and phylogeny of the primates. The poverty of

primate paleontology as compared with that of certain other mammalian orders is undoubtedly to a large degree a reflection of the habits and habituses of primates, which do not favor preservation of these animals as fossils. Notwithstanding, as Dr. Patterson points out, paleontology is in a position to make certain reasonable suggestions. It is impossible for me even to note, much less discuss, all of the interesting points that have been raised in his stimulating paper; so I will confine myself to a few that seem particularly pertinent.

Dr. Patterson is inclined to agree with Barth that in early Tertiary times the differences between lemuroids and tarsioids were not very important. This might be interpreted as indicating a late separation of the two groups, a view that seems recently to have gained in popularity; but, as Dr. Patterson notes, the history of the so-called prosimians is far from clear.

I am extremely interested in Dr. Patterson's appraisal of those late Eocene and early Oligocene catarrhines termed, respectively, *Amphipithecus, Moeripithecus, Parapithecus, Propliopithecus,* and "*Kansupithecus,*" all known only by their lower jaws. As he states, they were "probably of the greatest importance in primate history"; but he is only being realistic when he advocates that they be listed simply as Catarrhina (or Anthropoidea) *incerta sedis.* To them might also be added *Oreopithecus,* with which Dr. Patterson has dealt so illuminatingly, and *Apidium.* Various theories, some of them smacking of dogmatism, and in general not warranted by the meager evidence that the specimens provide, have been spun around these fragments. It is better to admit, as Dr. Patterson intimates, that the origins and early history of the catarrhines are still largely shrouded in mystery.

Dr. Patterson has shown us two diagrams of primate phylogeny, one by Dr. A. H. Schultz and one by himself. That these diagrams, each by an outstanding student of primates, can differ so strikingly in so many important points, is highly significant. It emphasizes the fact that in the present state of our knowledge it is quite possible to arrive at very different interpretations of primate history. It can scarcely be doubted that future paleontological discoveries will bring about important and perhaps even startling changes in our concepts of primate phylogeny.

I fully endorse Dr. Patterson's appraisal of the available evidence as indicating that "extreme brachiation was a very late event in catarrhine evolution." But when he suggests that preadaptation to brachia-

tion was peculiar to the pongid or hominoid stock, which gave rise to the existing anthropoid apes and man, I cannot quite go along with him. I do not intend to discuss the moot question of whether there was a brachiating stage in man's ancestry; for this symposium is primarily dedicated to the nonhuman primates. Furthermore, as I have pointed out elsewhere, the matter of semantics is involved, in that the term "brachiation" does not mean the same thing to all students. However, I wish to note that bimanual progression is not limited, among the catarrhines, to the pongids. Some of the living cercopithecine monkeys swing by the arms on occasion and hence might well be regarded as primitive brachiators; and the semnopithecine monkeys, especially *Colobus*, are even more addicted to this type of locomotion. Thus I submit that the penchant for occasional or moderate arm-swinging, or call it "brachiation" if you will, probably was common to the whole of the catarrhine stock rather than restricted to the pongid or hominoid radiation as Dr. Patterson suggests. That acceptance of this concept might alter one's views on the phylogeny of the catarrhines, surely need not be emphasized here.

I wish that there were time to discuss Dr. Davis' paper at length, for it is full of stimulating ideas. He rightly insists that the central problem of comparative anatomy, and of historical biology in general, is to explain—rather than simply to describe—the events of organic evolution. His emphasis on genetics and morphogenetic fields is in line with the concepts of the newer comparative anatomy. Dr. Davis believes that mutations having relatively major phenotypic effects have played a part in evolution. This belief, as he realizes, represents a scientific heterodoxy with which, however, I am personally inclined to agree. His insistence that structure cannot be divorced from function, and that comparative anatomy is sterile without this dual emphasis, represents a repudiation of the still dominant Gegenbaurian concept of comparative anatomy—a repudiation to which I heartily subscribe. Dr. Davis has presented a method for the sorting out of morphological characters into categories, separating the phylogenetically old from the phylogenetically new. Although this procedure is scarcely new in comparative anatomy, yet that some such evaluation is necessary and needs reemphasis is of course obvious. But when it comes to labelling characters as "heritage" or "habitus" traits, I can only repeat what I said in 1949: "This method might be valid were we able, with any degree of conviction, to separate characters into such distinct categories. . . Furthermore, it is

exceedingly doubtful whether such a separation is justifiable, if for no other reason than that it remains to be proven for any character that it is not in some way adaptive. Even assuming that there is such a truly fundamental distinction, there is every reason to believe that gene complexes underlie both such kinds of characters." Finally, Dr. Davis' emphasis on the importance of studying the treeshrews and the generalized insectivores in attempting to understand human evolution is in line with what has already been said. Students of man's evolution cannot stop with man, nor even with the primates. The whole of mammalian history, even of vertebrate history, has left its mark upon him. Hence the anthropologist needs a broad comparative point of view.

Aside from the light that they cast on existing forms, the papers of Drs. Schuman and Brace, Dr. Tappen, and Dr. Erikson in this symposium provide data of great value in the interpretation of the remains of fossil primates in general; they also are of particular value in interpreting the vestiges of human evolution.

The detailed study of Drs. Schuman and Brace of the variability of the permanent teeth in a representative population sample of the Liberian chimpanzee, with its valuable statistical analysis, constitutes a truly major contribution. As Dr. Hooton has pointed out, and as I have noted elsewhere, sweeping phylogenetic conclusions derived from dental morphology have all too often been based upon inadequate knowledge of dental variability, whether this variability be intrageneric, intraspecific, or at a lower taxonomic level. Primate taxonomy, whether one likes it or not, is, largely because of paleontological necessity, primarily a dental one. Yet, detailed knowledge of normal dental variability in primates is shockingly inadequate. Thus, as I have said elsewhere, and which I now repeat with apologies, "it is not improbable that undue emphasis has often been placed upon slight differences in dental morphology, with consequent taxonomic or phylogenetic interpretations that would not have been drawn had more information regarding the dental variability of the involved form or forms been available." The study of Drs. Schuman and Brace, the importance of which can scarcely be overstressed, helps fill in one of the many yawning gaps in our knowledge of primate dentitions; in doing so, it demonstrates the high degree of dental variability that can occur within a homogeneous primate population—a demonstration which, it is to be hoped (though perhaps I am overoptimistic), may serve as a rein upon unbridled odontological speculation. It is also to be hoped that this study will

provide a stimulus for further studies of this sort. It would be particularly instructive to compare Drs. Schuman and Brace's group of chimpanzees with that other large and homogeneous sample from a totally different locality belonging to the Todd Collection of Western Reserve University.

Dr. Tappen's split-line studies of the orientation of Haversian systems within the skulls of representative primates is an example of the application of one of the newer techniques to a dynamic analysis of the skeleton—a type of approach for which anthropology is largely indebted to Dr. Washburn. Despite the limitations admittedly inherent in this particular technique—namely, its restriction to the more external details of bony structure—it has already yielded basic information respecting at least some of the factors involved in the forms of bones, and the contributions possible by this method are almost innumerable.

I have followed Dr. Erikson's long-term study of the New World monkeys with great interest; for the platyrrhines represent an important and relatively neglected primate group. Although almost nothing is known of their geological history, as Dr. Jepsen has pointed out, there nevertheless is little or no reason to doubt that they have long pursued their own course of evolution quite independent of the catarrhines and that the numerous, intriguing similarities between the two simian groups represent autonomous developments. Because of these striking parallelisms the platyrrhines assume a somewhat strategic position for providing data that can aid in elucidating the phylogenetic relationships of catarrhine groups. Detailed knowledge of platyrrhine morphology and its relations to ecology and physiology, both locomotor and otherwise, will certainly aid in the analysis and interpretation of the several and somewhat diverse types of brachiation that have evolved, apparently quite independently, in various Old World simians. Indeed, it may well throw light upon that important and vexed question, already noted above: "What role, if any, did brachiation play in the evolution of man?" As Dr. Erikson notes, the majority of studies of human phylogeny have been too exclusively restricted to men and anthropoid apes and too narrowly focussed on the skeleton, especially on the skeleton of the head. From the point of view of primate paleontology, his studies are of particular significance for any analysis of the functional characters of postcranial skeletal remains. Also of great importance to students of human phylogeny is the emphasis that Dr. Erikson places, and rightly so, I believe, upon the necessity of truly recognizing the existence of the

phenomenon of parallelism. And, finally, which should provide anthropologists and paleontologists with food for thought, there are the disharmonies and puzzles that he notes—such disharmonies and puzzles as the association of seemingly similar morphological patterns with very dissimilar habituses, and the reverse. Although his particular analysis relates to New World simians, it is obvious that this type of study is also quite applicable to the simians of the Old World.

It is beyond my capacity to analyze critically the papers of Drs. Carpenter, Nissen, Harlow, and Hayes. But there are several comments that I would like to make.

Dr. Carpenter's paper underlines the importance of field studies of nonhuman primates, like those that he has already made on howlers, on spider monkeys, on macaques, and on gibbons, like that of Dr. Nissen on chimpanzees and like that of Dr. Zuckerman on baboons. I can only echo Dr. Hooton's plea for more studies of the social life of contemporary nonhuman primates in natural environments; and I likewise deeply deplore the virtual cessation of such studies. For, like Dr. Hooton, I am convinced that studies of this sort are more likely to illuminate the origins and evolution of human social organization and behavior than are studies of "primitive" or "uncivilized" human groups. And I say this without intending at all to deny the value of the latter type of study.

The papers of Drs. Nissen and Harlow stress the importance of nonhomeostatic and, at times, apparently purposeless motivation in primate behavior—such things as play, exploration, and curiosity. This may possibly be something that is essentially peculiar to primates, at least in the degree of its development. To express it in the language of a layman, it is what I like to call the "cussed curiosity" of primates, at least of simian primates. I strongly suspect that this "cussed curiosity" is even more highly developed in Old World simians than in New World simians, although I cannot support my suspicion by controlled observations. If this is actually true, it may well explain why it fell to the lot of the Old World simians to produce a cussedly curious, cantankerous, highly individualistic, and successful creature such as man, with all of his appurtenances that collectively go to make up the phenomenon which passes under that vague term, "culture."

Psychobiological studies, such as those discussed in this symposium, prove, quite as definitely as morphological ones, that man is a primate and, more particularly, a catarrhine primate. But, effective as they are

in providing knowledge of the raw materials that go to make up human behavior, they still fall short of explaining that great behavioral difference between man and those animals that Dr. Hooton has so pungently termed "man's poor relations." I was about to say that the difference is one of culture; but "culture" is a word that has been bandied about and which is difficult to define, as the paper of Dr. and Mrs. Hayes so clearly demonstrates. Man's prime behavioral peculiarity and his greatest distinction resides in the fact that he is a time-binder and a tool-maker. The former may be merely a matter of degree when comparison is made with other animals, but the fact remains that man is peculiar in the extent to which he lives in the three dimensions of time. It is this peculiarity that gives rise to his remarkable degree of foresight or anticipation which is perhaps best expressed in tool-making, to use this term in its broadest sense. And it is tool-making—not tool-using, as the Hayeses seem to believe—that represents the greatest distinction of man. It is the expression of the capacity of men for making—to borrow Dr. Nissen's words—"long-range plans by which our ultimate goals are more efficiently approached." The actual basis of this human trait remains to be determined. That it is largely neurological, there seems little doubt. Yet to deny morphological and physiological changes in other parts of the body an important role in the evolution of human behavior as the Hayeses would seem to do, strikes me as unrealistic and naive. It is more than difficult to believe that non-neural structures do not also play a role in the determination of behavior. Thus, as I have stressed elsewhere, the happy combination of an adequate brain and an adequate hand undoubtedly played a major role in determining the course of human evolution.

The hypothesis of Dr. and Mrs. Hayes regarding the origin and early evolution of human behavior is an interesting one, which, at the present time, can be neither proved nor disproved. Their argument is beclouded, however, by resort to that vague term, "culture," which, as Dr. Hooton has noted, is virtually undefinable.[1]

[1] During the discussion at the Wenner-Gren Foundation International Symposium on Anthropology held in June, 1952, I suggested that man may be defined as "an animal possessing a culture" (see *An Appraisal of Anthropology Today*, 1953, pp. 262-264). Subsequently, it has been amply demonstrated that the term "culture," even in its application to present-day human groups, is used inconsistently by anthropologists and without general agreement as to its precise meaning. The recent reviews of Kroeber's *The Nature of Culture* and Kroeber and Kluckhohn's *Culture: A Critical Review of Concepts and Definitions* by

It is far from my intention to belittle the importance of the truly fine contributions that have resulted from psychological studies of chimpanzees. Nor do I wish to impugn Dr. and Mrs. Hayes' interesting study of Viki. But it should always be remembered that it is unwise to place undue emphasis upon an organism that may well be, insofar as the evolution of man is concerned, deviant. The assumption of Dr. and Mrs. Hayes that "man's ancestry includes, at some stage, a species which was physically and behaviorally similar to the modern chimpanzee—in a general way, if not in detail," is, in the light of present knowledge, certainly open to serious question. That the chimpanzee is adapted to a peculiar mode of life, involving morphological and physiological specializations of a high order, is not to be seriously doubted. And that there consequently are accompanying behavioral specializations must be taken for granted. The concept of a "chimpanzee" stage in human evolution is, to put it mildly, a bit atavistic—it is downright Haeckelism.

I have found it somewhat disturbing to hear the psychologists use such terms as "phylogenetic scale," "phylogenetic level," and "higher" and "lower." It is difficult for me to believe that they use these terms seriously. In any case, we had best abandon such terms. For we shall never truly understand human evolution if we think in terms of a *scala naturae*—no more so than if we think in terms of a "great chain of being."

In closing, I can only emphasize that anthropology is by nature a highly eclectic science. It is far too broad in scope to be adequately mastered by any one person. Therein lies its strength, for it serves as a focal point for workers in many fields. The symposium just completed amply attests to this.

Leslie A. White and Joseph H. Greenberg, and of *Anthropology Today* and *An Appraisal of Anthropology Today* by Wilson D. Wallis (*Am. Anthropologist*, vol. 56, no. 3, June 1954) make this quite evident. The term "culture" remains particularly "vague" and "virtually undefinable" when applied to the comparative study of behavior within the order Primates.

INFORMATION FOR CONTRIBUTORS

HUMAN BIOLOGY, a record of research, is a quarterly journal devoted to the subject its name implies. It publishes original articles dealing with human genetics, development, growth, reproduction and aging, functional anatomy, bio-anthropology, human ecology, population dynamics, etc.

The original manuscripts, typed double-spaced on one side of 8½ x 11 inch paper in complete and finished form generally suitable for publication, should be sent—packed flat—to the editor, Dr. Gabriel Lasker, Wayne University College of Medicine, 1401 Rivard Street, Detroit 7, Michigan. It is desirable that a second copy be included in order to expedite prompt consideration, and that an additional carbon copy and copies of all illustrations should be retained by the author.

Where possible, illustrations should be made for reproduction as line engravings, hence drawn in India ink as boldly as possible. Lettering must remain legible after figures are reduced to fit on 4½ x 6½ inch pages (letters 1½ to 2 mm high after reduction are adequate). Figures should be numbered consecutively with Arabic numerals. Tables should be numbered independently from 1 up, and both figures and tables should have captions. When the amount of tabular and illustrative material is judged to be excessive or unusually expensive, authors may be requested to pay the excess cost. Galley proofs will be sent to the author and must be returned promptly; when the author makes substantial departures from copy, the cost will be charged to him. Three copies of an abstract (not to exceed 225 words) should be submitted when the proof is returned. One will be sent to the editor of *Biological Abstracts*.

References in the text to the literature should be made by using the author's name followed by the year of publication: "Studies of Garn and Saalberg ('53) . . ." At the end of the article, under the heading "LITERATURE CITED," full references with titles and inclusive page references should appear (double spaced) in alphabetical order of the authors' names: "GARN, S. M. AND J. F. SAALBERG 1953 Sex and age differences in the composition of the adult leg. Human Biol., 25: 144-153."

Authors will receive 25 free reprints. Orders for additional reprints should be placed at the time proof is returned. It may not be possible to accept orders for reprints after the proof has been returned to the press.

Human Biology

a record of research

VOLUME 26 SEPTEMBER 1954 NUMBER 3

CONTENTS

THE NON-HUMAN PRIMATES AND HUMAN EVOLUTION

A DEDICATION. *James A. Gavan*

THE IMPORTANCE OF PRIMATE STUDIES IN ANTHROPOLOGY. *Earnest Hooton* 179

FOSSIL PRIMATES IN THE NEW WORLD. *G. L. Jepsen* 180

THE GEOLOGIC HISTORY OF NON-HOMINID PRIMATES IN THE OLD WORLD. *Bryan Patterson* 191

COMPARATIVE ANATOMY OF NEW WORLD PRIMATES AND ITS BEARING ON THE PHYLOGENY OF ANTHROPOID APES AND MEN. *G. E. Erikson* 210

PRIMATE EVOLUTION FROM THE VIEWPOINT OF COMPARATIVE ANATOMY. *D. Dwight Davis* 211

A COMPARATIVE FUNCTIONAL ANALYSIS OF PRIMATE SKULLS BY THE SPLIT-LINE TECHNIQUE. *W. C. Tappen* 220

METRIC AND MORPHOLOGICAL VARIATIONS IN THE DENTITION OF THE LIBERIAN CHIMPANZEE, COMPARISONS WITH ANTHROPOID AND HUMAN DENTITIONS. *B. L. Schumer and C. L. Bruce* 239

TENTATIVE GENERALIZATIONS ON THE GROUPING BEHAVIOR OF NON-HUMAN PRIMATES. *C. R. Carpenter* 262

PROBLEMS OF MENTAL EVOLUTION IN THE PRIMATES. *Henry W. Nissen* 277

THE CULTURAL CAPACITY OF CHIMPANZEE. *Keith J. Hayes and Catherine Hayes* 283

CLOSING REMARKS. *William L. Straus, Jr.* 304

WAYNE UNIVERSITY PRESS, *Publishers*

DETROIT 1, MICHIGAN, U.S.A.